Fishery Bulletin

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Seattle, Washington

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VALIDATION OF THE OTOLITH INCREMENT AGING TECHNIQUE FOR STRIPED BASS, *MORONE SAXATILIS*, LARVAE REARED UNDER SUBOPTIMAL FEEDING CONDITIONS

CYNTHIA JONES[1] AND EDWARD B. BROTHERS[2]

ABSTRACT

Striped bass, *Morone saxatilis*, larvae were reared in the laboratory for 97 days to validate the otolith increment aging technique for this species. Otolith-increment deposition rates were determined under optimal laboratory conditions for growth and under three conditions of restricted feeding and using both light and scanning electron microscopy (SEM). Under optimal laboratory conditions, increments were deposited daily from the fourth day after hatching through the first 2 months of life and were discernible with the light microscope. For larvae reared under restricted feeding regimes and readings done with the light microscope, counts did not reflect true age. Counts obtained from these same otoliths using SEM, however, more closely reflected true daily age. Results indicate that the use of light microscopy alone can result in inaccurate estimation of age for larvae that have experienced starvation episodes.

When otolith increments in larval fish are deposited daily, with a known time of onset, precise age of each individual can be determined and the growth curves for the individuals may be generated. The ability to follow changes in growth of individuals and populations on as fine a scale as, say, a week may provide a means to improved understanding of the effects which environmental factors have on survival.

To apply this aging technique to larval striped bass, *Morone saxatilis*, daily deposition of increments and the age at first increment deposition had to be confirmed in the laboratory with known-age larvae. Although daily depositional rates of otolith increments in known-age larval striped bass have not been previously reported, daily deposition has been noted for larvae and juveniles of 17 other species of fish reared in the laboratory (see Jones 1985 for review). Nonvalidated data exist to support the concept of daily increment deposition for field-captured striped bass (Brothers et al. 1976). However, tests of depositional rate under suboptimal laboratory conditions, using light microscopy, have shown that depositional rates can be affected by the specific growth rate (Geffen 1982), by photoperiod (Radtke 1978), by food supply (Geffen 1982; Neilson and Geen 1982), and by temperature (Brothers 1978; Geffen 1983). Campana and Neilson (1985) stated that "few workers have critically assessed the assumptions upon which the age and growth inferences are based or considered the potential for environmental modification of microstructural features."

Of particular importance is the potential for counting fewer otolith increments when otolith growth rate is slowed to the extent that increments being deposited are too narrow to resolve with a light microscope. Inadequate resolution with the light microscope could lead to systematically low increment counts and thus, result in overestimation of the growth and mortality rates, and underestimation of variance in growth, all of which have important biological implications. Hence, to demonstrate that striped bass larvae from the field could be aged accurately by the otolith increment technique, we found it necessary to determine the regularity and readability of otolith-increment deposition under simulated laboratory suboptimal field conditions.

Lack of scanning electron microscopy (SEM) validation hinders the resolution of an important issue: Is daily formation of increments a robust biological rhythm common to most teleosts which requires serious and prolonged starvation to disrupt, or is it a more volatile physiological connection in which daily formation occurs only under optimal food concentrations as certain laboratory studies indicate?

Factors which affect growth and survival of striped bass larvae have been studied extensively (see Westin and Rogers 1978 for review). Rogers (1978) raised larval striped bass under various temperature and feeding regimes to determine growth under laboratory conditions. Larvae grew well at

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temperatures between 16° and 22°C and with a minimum of 1,000-2,000 *Artemia* nauplii/L. The optimum salinity range was between 3.5 and 14.0‰ (Bayless 1972). Davies (1973) studied larval survival under combinations of temperature, pH, and dissolved solids. Optimum temperature was 17.0°C; optimum pH, 7.5. Eldridge et al. (1981) studied the growth of larvae under various feeding regimes and found growth rates which approximated field growth rates at concentrations of 5,000 *Artemia*/L. They found that the "point of no return" was ill defined and starved larvae could live for as long as 31 days. Dey (1981) has reported on growth and survival of wild larvae, using length and developmental stage to estimate growth. He found growth was temperature dependent and temperatures between 12° and 15°C resulted in massive mortalities.

The purpose of this study was to determine the relationship between age, environmental condition, and otolith increment depositional rates in laboratory-raised striped bass larvae. This was accomplished by studying the increments of known-age larvae reared under both optimal laboratory conditions and restricted feeding regimes (laboratory-simulated suboptimal field conditions). Larvae were subjected to various periods of food deprivation to determine the potential dependence of increment depositional rates on nutritional condition. Specifically, incremental counts made with light microscopy and SEM were compared to evaluate the reality of apparent interruptions of daily deposition.

METHODS

Striped bass eggs were obtained from the Verplank Hatchery, Verplank, NY, within 24 hours of fertilization. Eggs were held in water obtained at the hatchery (0‰ salinity) at 18°C, under a 14L: 10D photoperiod. Light levels were 25-31 μ Einsteins/m^2 per second. This light level is approximately equal to light at a depth of 2-3 m in a coastal stream or 1 m in a coastal estuary depending on turbidity and season of the year. Eggs hatched within 24 hours of fertilization. Newly hatched larvae were transferred to 4 L jars and stocked at densities of 50 per liter. Over the first 8 days, salinities were gradually raised to 5‰ by adding filtered seawater with 0‰ water. Seventy-six days after hatching of the larvae, salinities were gradually raised to 10‰ over a span of 8 days. Water was changed at least every other day.

Four feeding conditions were established. The food for all conditions was newly hatched brine shrimp, *Artemia*. Larvae were fed ad libitum (condition 1), other larvae were starved throughout the experiment (condition 2), and other larvae were starved for the first 15 days after hatching, then fed ad libitum (condition 3). Condition 4 consisted of larvae that were intermittently deprived of food. These larvae were not fed between 39-43, 51-55, and 62-66 days after hatching, for a total of 15 days out of the 68 days they were reared. For the remaining time they were fed ad libitum.

Larvae were sampled according to the schedule listed in Table 1. Larvae that were sampled were anesthetized with Tricaine methanesulfonate (Cresent Research Chemical[3]) and sacrificed. Total length was measured to the nearest 0.1 mm. Otoliths were teased from the otic capsules with fine dissecting needles, cleared of tissue, washed in deionized water and transferred with a micropipette or with fine dissecting needles to a labeled microscope slide.

Small otoliths were mounted permanently in *Euparol* without grinding. Larger otoliths were mounted in Flowtex (Lerner Laboratories), ground with 600 grit sandpaper and read with the light microscope. A subsample of ground otoliths was removed from the Flowtex, mounted in Spurr's medium, and ground to the core on Beuhler lapidary wheels. Initial grinding on the wheels began at 180

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sample size at age of striped bass larvae reared under four feeding regimes. N.T. = not taken.

Age (d)	Feeding regime condition			
	Continuously fed	Starved	Starved then fed	Intermittent starved
3	3			
4	8	5		
5	5	3		
6	5	5		
7	5	5		
8	5	5		
9	5	5		
10	5	5		
14	5	5		
18	5	5	2	
22	5	5	2	2
26	5	6	2	2
33	5		2	2
38	4		N.T.	N.T.
40	2		3	2
47	5		2	2
54	5		2	2
58	1		N.T.	N.T.
64	N.T.		1	N.T.
68	3		3	2
97	5		2	

grit and final polishing was done with 0.25 μm diamond paste. These otoliths were etched with 0.02N HCl, then mounted on SEM stubs and sputter coated with gold/palladium.

Three light microscopes were used: a Zeiss, a Leitz, and an Olympus. The latter two were equipped with video viewing systems and polarized light sources. Readings were done with brightfield illumination at 400, 540, and 1,000 power. Video increased magnification to a maximum of 2700×. The maximum resolution for the light microscopes was 0.5-1.0 μm. The SEM employed was a JOEL (JSM 200) equipped with both secondary electron image (SEI) and backscattered electron image (BEI) collectors.

For light microscopy, slides were chosen at random and read double blind (age of the larvae and condition were unknown). Readings were done three times for each slide. Each slide was counted only once during each session so that replicate counts did not immediately follow each other. Thirteen of the twenty-four samples from conditions 3 and 4 were used for SEM analysis. For SEM examinations, counts were blind (ages of the larvae were unknown); condition, however, was selected by the investigators to check the accuracy of the light microscope counts for conditions 3 and 4.

RESULTS

Light Microscopy

The relationship between the number of otolith increments and age, in days, for the four experimental conditions is shown in Figure 1. Fully fed larvae (n = 63), condition 1, had a regression slope of 0.98 increments/day, and the smallest standard error (Table 2). Its confidence interval included 1 increment/day. Beyond 68 days of age sagittae became very difficult to read. Continuous counting paths or an appropriate series of transects were difficult to find because the sagitta changes shape and develops new centers of deposition around the periphery of the otolith. This resulted in underestimates of true age (Table 2) for larvae older than 2 months of age.

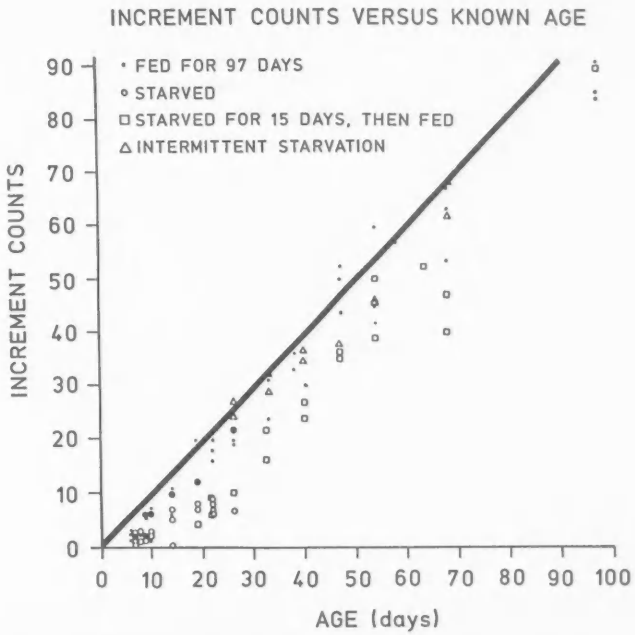

FIGURE 1.—Relationship between otolith increment count in larval striped bass and true age for four feeding regimes, light microscope observations.

TABLE 2.—Parameters for weighted regressions of increment counts on days from hatch of striped bass larvae reared under four feeding regimes. SE indicates standard error of the estimate, C.I. indicates confidence interval, N.S. indicates slope not significantly different than 1.0, * indicates $P = 0.05$.

Age	Condition	N	Slope (counts/d)	Slope SE (slope)	95% C.I. Low	95% C.I. High	Intercept Counts	Intercept SE (int)	r^2	$P > 0.05$
68 d and younger	1 Always fed	60	0.980	0.0243	0.931	1.029	−4.016	0.4482	0.96	N.S.
All ages	1 Always fed	63	0.946	0.0169	0.912	0.980	−3.627	0.4068	0.96	*
	2 Starved	43	0.469	0.0402	0.388	0.550	−1.697	0.4325	0.77	*
	3 Starved/fed	12	0.930	0.1005	0.711	1.149	−10.430	4.3906	0.90	N.S.
	4 Intermittent	12	0.873	0.0586	0.745	1.000	2.579	2.4010	0.96	N.S.

The slope of the regression line for starved larvae (condition 2, $n = 43$), 0.469 increments/day, differed significantly from 1.0 increment/day. Increments appeared regularly spaced. Otoliths of starved larvae did not appear aberrant under the light microscope.

The regression of increment counts versus true daily age for larvae, which were starved then fed (condition 3, $n = 12$), had a slope of 0.930 increments/day with confidence intervals which included 1.000 increments/day (Table 2). However, the regression intercept was −10.430, an overestimate of age at first increment deposition. This leads to a 6-d underestimate of true age because depositional rates were underestimated during the first 2 weeks of life.

The slope of the regression line for intermittently starved larvae (condition 4, $n = 12$) was 0.873 increments/day. The slope of 1.0 increment/day fell at the very edge of the confidence interval. If a slightly smaller alpha level had been chosen, deposition would not have been assumed daily.

Initial increment formation began at 4 days after hatching with a 95% confidence interval that ranged from 3 to 5 days. Yolk-sac absorption occurs at 7 days after hatching at 18°C and first feeding begins at approximately the same time. However, initial increment deposition does not appear to be connected to these events. Two or three weakly defined increments were observed within the core in many SEM preparations. They were not counted in light or SEM readings.

Scanning Electron Microscopy

Results from the SEM study are qualitative rather than quantitative due to the small sample sizes, $n = 13$, used for the SEM. With SEM, otolith increment counts for condition 3, larvae which were starved then fed (Table 3), and for condition 4, larvae which were intermittently starved (Table 4), yielded more accurate counts than those obtained on the same specimens with light microscopy. With light microscopy counts from larvae which were starved for 15 days resulted in an underestimate of true age by 10 days (Table 3). The variability was also high (SE = 7.9 days). SEM counts underestimated true age by 2 days. Variability was small; the standard error was 3.4 and 4.0 days for SEI and

TABLE 3.—Counting bias for larvae starved for the first 15 days after hatch (calculated as estimated age − true age[1]). Underestimate of age is indicated by −; overestimate indicated by +. SEI = secondary electron image; BEI = backscattered electron image.

Sample no.	Age (d)	Microscopic technique Light	SEI	BEI
1	68	−17	0	+1
2	47	− 7	−5	−5
3	54	0	−5	−6
4	68	−24	−5	−5
5	33	− 7	+4	+5
6	47	− 8	−2	−2
7	47	− 7	−1	0
Mean bias		−10	−2	−2
SE		7.9	3.4	4.0

[1]Estimated age = number of increments + mean age at first increment formation.

TABLE 4.—Counting bias for larvae intermittently starved (calculated as estimated age − true age[1]). Underestimate of age is indicated by −; overestimate indicated by +. SEI = secondary electron image; BEI = backscattered image.

Sample no.	Age (d)	Microscopic technique Light	SEI	BEI
8	68	+ 2	−5	−6
9	47	− 5	−5	−3
10	54	−11	−1	−2
11	54	− 4	−4	0
12	47	+ 2	−4	−4
13	47	− 5	+1	+1
Mean bias		− 4	−3	−2
SE		4.9	2.4	2.6

[1]Estimated age = number of increments + mean age at first increment formation.

BEI, respectively. Light microscope-counted increments of intermittently starved larvae underestimated age by 4 days (Table 4). The standard error of the mean was 4.9 days. For this sample, both SEM techniques also gave more accurate age estimates. SEI underestimated age by 3 days (SE = 2.4 days), and BEI underestimated age by 2 days (SE = 2.6 days).

The comparison between SEI and BEI showed no significant difference in accuracy (Tables 3, 4). Figures 2A and 2B illustrate the increment structure observed with these two methods of SEM. BEI

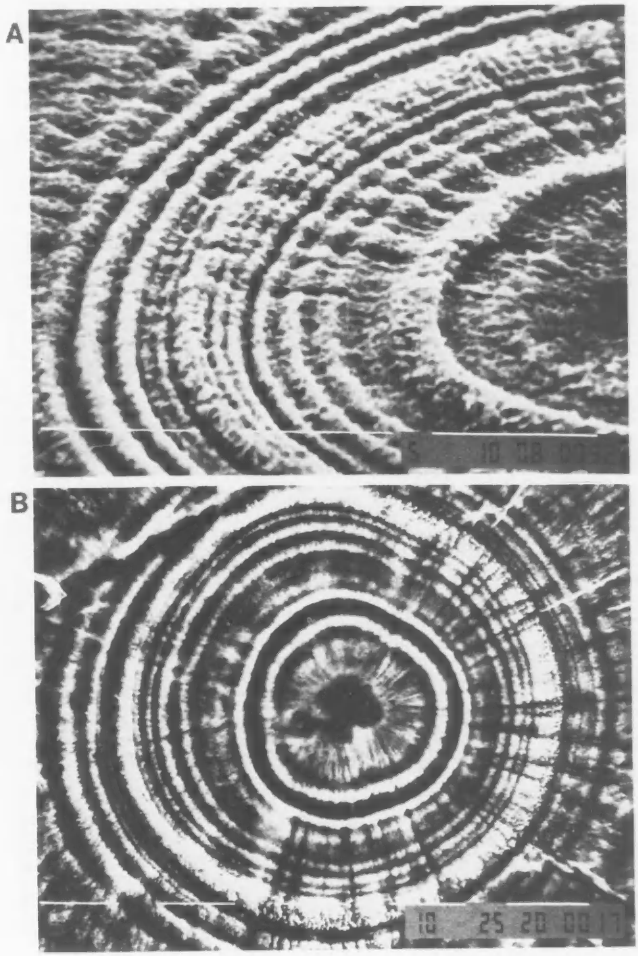

FIGURE 2.—Comparison of otoliths of larval striped bass using two scanning electron microscope (SEM), techniques. A) Normal secondary emission (SEI) photomicrograph of an otolith of a larva starved for the first 15 days posthatch then fed ad libitum until sacrificed. Increment width during starvation is approximately 5 μm. B) Backscattered emission (BEI) photomicrograph for a comparable otolith to A above. Legends in the micrographs indicate 1) length of scale bars in μm, 2) accelerating voltage KV, 3) mm working distance, 4) coded photo number.

enhances contrast, but does not allow the specimen to be tilted. With SEI, tilting can increase increment relief and visibility.

Increments deposited during starvation were only 0.5 μm in width, too closely spaced to be discerned with the light microscope (Fig. 3). Additionally, the material that is deposited appears to be more homogenous in density, probably containing a lower amount of matrix. When etched, less material was dissolved in the area corresponding to starvation periods. This resulted in a higher area of relief, forming a broad ridgelike structure, subdivided into finer increments. The etching properties were, therefore, different compared to the same area in the otolith of a fed larvae. This ridgelike structure consistently indicated periods of starvation during the first 2 weeks of life. Ridges were not apparent for older larvae starved for shorter time intervals (Fig. 4).

DISCUSSION

Estimation of age obtained using the light microscope was not always accurate. When larvae grew well, the light microscope gave correct age estimates. However, otoliths of larvae reared under suboptimal feeding conditions gave underestimates of true age. Age estimates were more accurate using SEM, and starvation episodes were easier to recognize in the otoliths.

Light microscopy has been routinely used to estimate age in field-captured larval fish (Jones 1985). Only a few investigators have employed SEM. Although SEM improves the accuracy of age estimates, it is more costly, requires more precise preparation, and is more time consuming. However, for larvae as resistant to starvation as striped bass, SEM verification of age estimation obtained with the light microscope is necessary. In our view, investigators using increments to estimate growth should check their results from the light microscope with SEM studies. SEM analysis could be performed on a randomly chosen subsample of otoliths. If problems were uncovered, a more extensive analysis using SEM could be undertaken. Checks on a random sample using SEM are particularly important for field studies where application of the otolith increment technique to estimate field growth is relatively new.

It could be argued that larvae which undergo periods of starvation are more vulnerable to predation and may occur only infrequently in samples. Although this is quite likely, it is precisely during

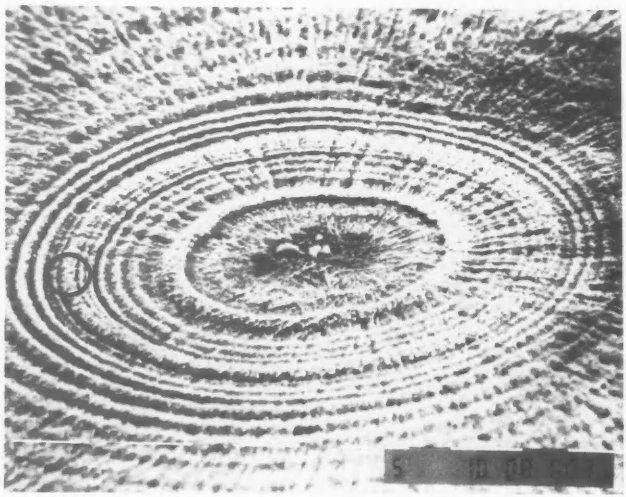

FIGURE 3.—SEM photomicrograph of an otolith of a larva starved for the first 15 days of life then fed ad libitum. A ridge, indicated by the circle, develops as the result of etching the otolith with 0.02 N HCl. This ridge corresponds to the period of starvation. Increment width during starvation is approximately 5 μm. Legends in the micrographs indicate 1) length of scale bars in μm, 2) accelerating voltage KV, 3) mm working distance, 4) coded photo number.

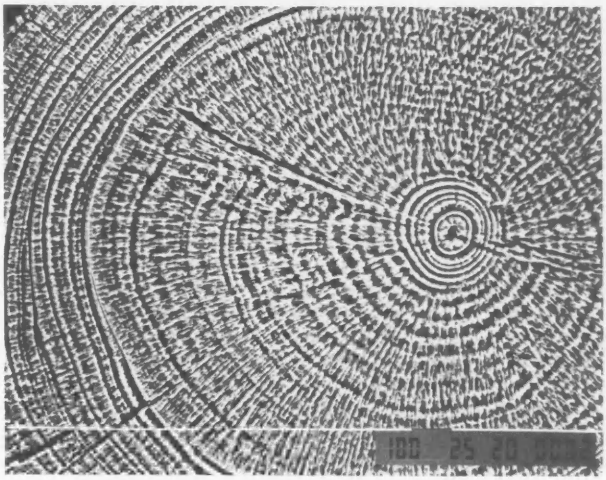

FIGURE 4.—SEM photomicrograph of an otolith of an intermittently starved larva. Note the pattern of narrow bands, indicated by the bracket, typical of starvation episodes. Increment width during starvation is approximately 5 μm. Legends in the micrographs indicate 1) length of scale bars in μm, 2) accelerating voltage KV, 3) mm working distance, 4) coded photo number.

years that have poor conditions, hence poor recruitment, that good age-based growth and mortality estimation would be the most useful. During such years, more of the young larvae could have their true age underestimated. This would result in overestimation of the abundance of younger larvae and therefore a steepened mortality curve. The best approach for routine field work may be to incorporate a design in which a small subsample of otoliths are analyzed by SEM to test for bias using the light microscope.

Bias in light microscope counts may account for the less-than-daily otolith increment deposition that has been demonstrated in the laboratory (Geffen 1982). For field-captured fish, there is no way of knowing whether light microscope counts are biased without the use of SEM. Additionally, this potential bias affects the variance of the estimate of size-at-age. When larval age is underestimated, under conditions which have resulted from poor growth, the variance is improperly decreased for young fish. Hence, lower variances may be a product of both high mortality and bias in age estimation.

Finally, the light microscope biases are more important for young larvae. By simple arithmetic, a bias of 3 days in a 7-d-old fish will result in a far more inflated growth rate than will a bias of 3 days (or for that matter 10 days) in a 60-d-old fish. The growth rate of the younger fish will be inflated 1.75 times compared with only 1.05 times (or 1.2 times using the 10-d bias) for the older fish.

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LITERATURE CITED

BAYLESS, J. D.
1972. Artificial propagation and hybridization of striped bass, *Morone saxatilis* (Walbaum). S.C. Wildl. Mar. Resour. Dep., Columbia, SC, 135 p.

BROTHERS, E. B.
1978. Exogenous factors and the formation of daily and subdaily growth increments in fish otoliths. [Abstr.]. Am. Zool. 18:631.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

CAMPANA, S. E., AND J. D. NEILSON.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014-1032.

DAVIES, W. D.
1973. The effects of total dissolved solids, temperature and pH on the survival of immature striped bass: a response surface experiment. Prog. Fish-Cult. 35:157-160.

DEY, W. P.
1981. Mortality and growth of young-of-the-year striped bass in the Hudson River Estuary. Trans. Am. Fish. Soc. 110: 151-157.

ELDRIDGE, M. B., J. A. WHIPPLE, D. ENG, M. J. BOWERS, AND B. M. JARVIS.
1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. Trans. Am. Fish. Soc. 110:111-120.

GEFFEN, A. J.
1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scopthalmus maximus*) larvae. Mar. Biol. (Berl.) 71:317-326.
1983. The deposition of otolith rings in Atlantic salmon, *Salmo salar* L., embryos. J. Fish. Biol. 23:467-474.

JONES, C. J.
1985. Determining age of larval fish with the otolith increment technique. Fish. Bull., U.S. 84:91-103.

NEILSON, J. D., AND G. H. GEEN.
1982. Otoliths of chinook salmon (*Oncorhynchus tshawytscha*): Daily growth increments and factors influencing their production. Can. J. Fish. Aquat. Sci. 39:1340-1347.

RADTKE, R. L.
1978. The formation and growth of otoliths in the estuarine fish, *Fundulus heteroclitus*. Ph.D. Thesis, Univ. South Carolina, Columbia, 57 p.

ROGERS, B. A.
1978. Temperature and the rate of early development of striped bass, *Morone saxatilis* (Walbaum). Ph.D. Thesis, Univ. Rhode Island, Kingston, 193 p.

WESTIN, D. T., AND B. A. ROGERS.
1978. Synopsis of biological data on the striped bass, *Morone saxatilis* (Walbaum) 1972. Univ. Rhode Island Mar. Tech. Rep. 67, 154 p.

OPTIMUM ALLOCATION FOR ESTIMATING AGE COMPOSITION USING AGE-LENGTH KEY

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ABSTRACT

A new optimum allocation method for age-length keys (ALK) was developed by applying Kimura's Vartot, an error index of estimated age composition. The method is applied to Pacific cod, sablefish, and walleye pollock. At the present working capacity, the total of 10,000 minutes (about 70 working days) will approximate the most effective cost to estimate age composition for the three species. Increasing costs beyond this level will show no more gain.

Age-length keys (ALK) are widely used for estimating age compositions in fisheries. The theory of ALK is based on a double sampling technique with stratification (Tanaka 1953). The first stage involves a simple random sampling for a relatively large size, less costly length sample. The second stage involves a stratified random sampling for a smaller size, more costly age subsample from each length stratum. Following the approximation of Kutkuhn (1963) and Southward (1963), the proportion of fish at the ith age class (p_i) and variance of p_i are estimated as

$$p_i = \sum_{j=1}^{L} l_j q_{ij} \quad (1)$$

$$\mathrm{Var}(p_i) = \sum_{j=1}^{L} \left[\frac{l_j^2 q_{ij}(1 - q_{ij})}{n_j} + \frac{l_j (q_{ij} - p_i)^2}{N} \right] \quad (2)$$

where l_j is the proportion of fish that fall into the jth length stratum,
N is total length sample size,
n_j is the size of age subsample in the jth length stratum,
q_{ij} is the proportion of n_j fish classified into the ith age class,
A is the number of age classes, and
L is the number of length strata.

Kimura (1977) defined Vartot as the sum of all variances of the p_i:

$$\mathrm{Vartot} = \sum_{i=1}^{A} \mathrm{Var}(p_i) = E\left[\sum_{i=1}^{A} (\hat{p}_i - p_i)^2 \right] \quad (3)$$

which is an error index for assessing precision of the ALK. Furthermore, Vartot is the expectation of the squared distance between the estimated age composition $\hat{P}' = (\hat{p}_1, \hat{p}_2, \ldots, \hat{p}_A)$ and the true age composition of the population $P' = (p_1, p_2, \ldots, p_A)$. Then, $D = \sqrt{\mathrm{Vartot}}$ can be interpreted as a kind of average Euclidean distance between $\hat{P}$ and P in an A-dimensional space. Kimura (1983) indicated that D can be viewed as the percent error of the estimated accumulated age proportion (i.e., the percent error of $\Sigma p_i = 1$).

This paper derives a new method for the optimum allocation of ALK, applying the properties of Vartot and Cauchy-Schwarz inequality (Kendall and Stuart 1977). The optimum sizes of length sample and age subsample are determined so that either Vartot is minimized subject to a fixed total cost or the total cost is minimized subject to a desired level of Vartot. Although this method is basically derived for the problem that all age classes are of equal interest, it can be modified by adding weighting factors to the ages which are important to population dynamics. This method was applied to Pacific cod, *Gadus macrocephalus*, from the Washington coast; sablefish, *Anoplopoma fimbria*, from the Gulf of Alaska; and walleye pollock, *Theragra chalcogramma*, from the eastern Bering Sea.

METHODS

Two subsampling schemes related to ALK are frequently used by fisheries biologists: 1) fixed age sub-

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sampling, in which the size of age subsample in all length strata is constant (i.e., $n_j = n/L$, where $n = \sum n_j$ is total age subsample size), and 2) random age subsampling, in which the size of the age subsample in each length stratum is proportional to the length sample size for all length strata (i.e., $n_j = nl_j$). Thus applying Equations (2) and (3), Vartot for a fixed age subsample (Appendix A) is

$$\text{Vartot} = \frac{a_1}{n} + \frac{a_2}{N} \tag{4}$$

and Vartot of a random age subsample is

$$\text{Vartot} = \frac{b_1}{n} + \frac{b_2}{N} \tag{5}$$

where $a_1 = \sum_{i=1}^{A} \sum_{j=1}^{L} [L\, l_j^2\, q_{ij}\,(1 - q_{ij})]$

$$a_2 = b_2 = \sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\,(q_{ij} - p_i)^2]$$

$$b_1 = \sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\, q_{ij}\,(1 - q_{ij})].$$

It should be noted that a_1, a_2, b_1, and b_2 are all positive values.

The total cost of a survey can be expressed as some function of the costs of the two sampling stages. The commonly used form of the cost function is a simple linear equation relating the unit cost of observing the length and the age of a fish to N and n (Tanaka 1953; Kutkuhn 1963; Southward 1963):

$$C = c_1 N + c_2 n \tag{6}$$

where C is the total cost, c_1 is the unit cost of observing the length of a fish, and c_2 is the unit cost of determining the age of a fish. For optimum allocation, the problem becomes one of determining the values of N and n, which will provide an estimated age composition with a minimum Vartot subject to a given total cost C.

Cauchy-Schwarz inequality, which is frequently used in sampling theory (Cochran 1977; Kendall and Stuart 1977; Schweigert and Sibert 1983), is applied to find optimum set of N^* and n^* for an ALK. The set of N^* and n^* is obtained when they minimize the product of D^2 (= Vartot) and C.

For a fixed age subsample, using Equations (4) and (6) and the Cauchy-Schwarz inequality (Appendix B), we obtain

$$r^* = (n/N)^* = \sqrt{a_1 c_1 / a_2 c_2}. \tag{7}$$

This quantity is the optimum subsampling ratio (r^*) required to reach the minimum (min.) Vartot subject to the cost function given in Equation (6). Therefore, N^* and n^* are dependent on Equation (6):

$$N^* = C/(c_1 + c_2 r^*) \tag{8}$$

$$n^* = r^* N^* \tag{9}$$

$$\text{min. Vartot} = \frac{a_1}{n^*} + \frac{a_2}{N^*}. \tag{10}$$

Similarly, the optimum allocation of a random age subsample can be obtained using Equations (5) and (6) and the Cauchy-Schwarz inequality. The solutions of r^*, N^*, n^*, and min. Vartot are

$$r^* = (n/N)^* = \sqrt{b_1 c_1 / b_2 c_2} \tag{11}$$

$$N^* = C/(c_1 + c_2 r^*) \tag{12}$$

$$n^* = r^* N^* \tag{13}$$

$$\text{min. Vartot} = \frac{b_1}{n^*} + \frac{b_2}{N^*}. \tag{14}$$

Generally, survey designs are based on two constraints (Schweigert and Sibert 1983). The first, as derived previously, relates to obtaining the precision of p_i, viz., to minimize Vartot at a fixed total cost. The second determines the total cost required to achieve a given precision, that is, to minimize total cost (min. C) at a desired level of Vartot. In the latter problem, r^* in Equations (7) and (11) will also minimize the product of D^2C irrespective of the value of C and D^2, i.e., it will minimize D^2 for fixed C or C for fixed D^2 (Kendall and Stuart 1977, Section 39.20). The solutions of n^* and N^* are now dependent on the desired level of Vartot.

For a fixed age subsample, substituting r^* of Equation (7) into Equation (4), we obtain

$$N^* = (a_1/r^* + a_2)/D^2 \tag{15}$$

$$n^* = r^* N^* \tag{16}$$

$$\text{min. } C = c_1 N^* + c_2 n^* \tag{17}$$

For a random age subsample, N^* is obtained by substituting Equation (11) into Equation (5)

$$N^* = (b_1/r^* + b_2)/D^2 \quad (18)$$

$$n^* = r^*N^* \quad (19)$$

$$\text{min. } C = c_1N^* + c_2n^*. \quad (20)$$

Because $0 < r \leq 1$, Equations (7) and (11) indicate that

$c_1/c_2 \leq a_2/a_1$ for fixed age subsample and

$c_1/c_2 < b_2/b_1$ for random age subsample

must be held for the optimum allocation. When equality holds, $r = 1$ and then ALK degenerates to a simple random sampling for age samples.

EXAMPLES

Three sets of ALK data are used for the example: Pacific cod, aged by the scale method, from the Washington coast (Kimura 1977); sablefish, aged by the otolith method, from the Gulf of Alaska; and walleye pollock, aged by the otolith method, from the eastern Bering Sea (Lai 1985). The parameters of Vartot, a's and b's, are calculated and summarized in Table 1. Accurate cost estimates are difficult to determine; therefore, time measurements required for observing a length and determining an age of fish are used for c_1 and c_2. The total cost C is thus the total time required to build an ALK. The measurements of c_1 and c_2 for the three species (Table 1) are primarily based on the author's experience.

Given a total of 120 working days and 6 working hours per day to a fisheries scientist, the optimum allocation is summarized in Table 2. Under this budget, a random age subsample can provide higher precision than a fixed age subsample (improved 10%, 15%, and 18% respectively for Pacific cod, sablefish, and walleye pollock). Also, for this budget, the error of estimated cumulated age proportion is less than 2.5% for the three species using either fixed or random age subsamples.

Using Equations (7), (15), (16), and (17) for a fixed age subsample and Equations (11), (18), (19), and (20) for a random age subsample, costs under various desired D are minimized for the three species (Table 3). At the same level of D, a fixed age subsample requires much larger sample sizes of length and age than a random age subsample does for the three species. The greatest benefit of using random age subsample is that it drastically reduces the total cost required to obtain the same level of D. The total cost is reduced by 35%, 45%, and 55% respectively for Pacific cod, sablefish, and walleye pollock for any given D when a random instead of a fixed age subsample is used.

Figure 1 shows the relationships of D and total cost. Whether a fixed or a random age subsample is used for the three species, it is obvious that D decreases rapidly until $C = 10{,}000$ minutes, which is nearly 70 working days. A point of diminishing

TABLE 1.—Parameters of Vartot and costs for optimum allocation.

	Pacific cod	Sablefish	Walleye pollock
a_1	0.4495	1.2222	1.5501
a_2	0.2660	0.1717	0.1217
b_1	0.2766	0.6235	0.6634
b_2	0.2660	0.1717	0.1217
[1]C	43,200	43,200	43,200
[1]c_1	0.5	0.5	0.5
[1]c_2	15	15	15

[1]In minutes, assuming 120 working days for each species and 6 working hours per day.

TABLE 2.—Optimum allocation of minimizing Vartot for Pacific cod, sablefish and walleye pollock. ($D = \sqrt{\text{Vartot}}$.)

	Pacific cod		Sablefish		Walleye pollock	
	fixed	random	fixed	random	fixed	random
N^*	10,641	13,121	5,534	7,555	5,093	7,551
n^*	2,525	2,443	2,695	2,629	4,064	3,943
D^*	0.014	0.013	0.022	0.019	0.020	0.017

TABLE 3.—Optimum allocation minimizing total cost for various desired precision level ($D = \sqrt{\text{Vartot}}$). Parameters and c_1 and c_2 are listed in Table 1.

		Pacific cod		Sablefish		Walleye pollock	
D		fixed	random	fixed	random	fixed	random
0.05	N^*	865	701	1,073	786	826	557
	n^*	206	130	523	273	659	291
	C^*	3,508	2,307	8,372	4,492	7,002	3,186
0.04	N^*	1,351	1,095	1,676	1,228	1,290	870
	n^*	321	204	817	427	1,030	454
	C^*	5,482	3,605	13,080	7,019	11,940	4,978
0.03	N^*	2,401	1,947	2,979	2,182	2,310	1,547
	n^*	570	362	1,451	759	1,831	808
	C^*	9,745	6,410	23,254	12,478	19,450	8,850
0.02	N^*	5,401	4,380	6,702	4,910	5,160	3,480
	n^*	1,282	815	3,265	1,708	4,118	1,817
	C^*	21,924	14,422	52,320	28,076	43,761	19,912
0.01	N^*	21,604	17,520	26,809	19,640	20,640	13,922
	n^*	5,121	3,262	13,059	6,832	16,473	7,269
	C^*	87,699	57,687	209,279	112,305	175,043	79,650

C^*: in minutes.

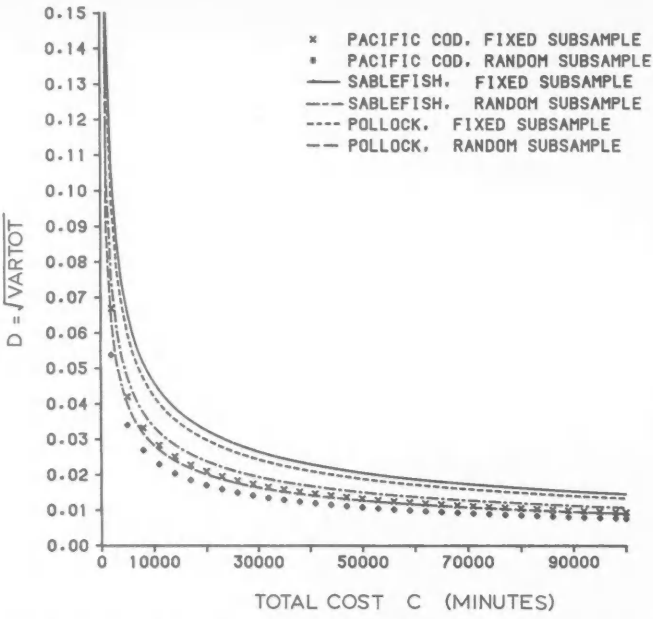

FIGURE 1.—The relationship of D ($= \sqrt{\text{Vartot}}$) and total cost for Pacific cod, sablefish, and walleye pollock, using fixed or random age subsample.

returns is reached beyond this total cost and the curves become flatter for C greater than 10,000. These results indicate that setting a precision at D = 0.02, 0.025, and 0.03 respectively for Pacific cod, walleye pollock, and sablefish using random age subsamples would represent a reasonable compromise between cost and precision. Increasing total cost beyond this level will show no more gains from the ALK.

DISCUSSION

It is obvious that the random subsampling scheme is superior to the fixed subsampling scheme. However, it is more important to realize that there is a cap on total cost for ALK. This cap represents the most effective budget for ALK. Vartot of estimated age composition will not decrease significantly for a greater budget. For the three species, total cost of 10,000 minutes (about 70 working days) is the upper limit. This indicates that approximately 2,000 length observations and 800 random age subsamples for sablefish, 2,500 and 1,200 for walleye pollock, and 3,000 and 600 for Pacific cod represent the best compromise between cost and precision of estimates ($\sqrt{\text{Vartot}}$ = 0.03, 0.025, and 0.02 for the three species respectively).

Although it can be argued that minimizing Vartot may not be sufficient for optimum sampling design for all age classes, it is necessary to consider that some age classes are rare in the commercial catch and are therefore difficult to sample precisely. However, these age classes do not generally represent significant contributions to biomass, and it therefore seems reasonable to concentrate on the major age classes. If these rare age classes are important to population dynamics, the optimum allocation can be addressed as a multiple minima. The objective function can be rewritten as

$$M(N,n) = \sum w_i \, \text{Var}(p_i), \qquad \text{for } i = 1, 2, \ldots, A$$

where w_i is weighting factor. A larger w_i must be given to those age classes which are of interest, whereas the mathematical expressions of optimum allocation are the same as Equations (7) to (14), and subject to the same cost function (Equation (6)), ex-

cept that a's and b's are weighted by w_i. In fact, minimizing Vartot is a special case of minimizing $M(N,n)$ = Vartot for all $w_i = 1$.

Another argument may relate to the possibility that the cost function may be more complicated so that traveling and overhead costs can be taken into account. In such cases, cost function may become a nonlinear form, and the explicit expressions of n^* and N^* cannot be obtained. However, the technique of nonlinear programming can be applied to find numerical solutions of n^* and N^*. In general, it is to

$$\text{minimize } M(N,n) = \sum w_i \operatorname{Var}(p_i)$$

$$\text{subject to } C = c(N,n)$$

where C is total cost and $c(N,n)$ is cost function. Many optimization programs can be employed from popular computer software packages for main frame computers. Bunday (1984) provided several BASIC programs for constrained optimization, which may be useful in personal computers. It should be noted, however, that the sufficient and necessary conditions of this constrained minimum must be proved. Theoretically, there is a unique minimum if objective function is convex and constraint function is concave (Bunday 1984).

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LITERATURE CITED

BUNDAY, B. D.
1984. Basic optimisation methods. Edwards Arnold, Lond., 128 p.

COCHRAN, W. G.
1977. Sampling techniques. 3d ed. John Wiley & Sons, Inc., N.Y., 428 p.

KENDALL, M., AND A. STUART.
1977. The advanced theory of statistics. Vol. 3. 3d ed. Griffin & Co., Lond., 585 p.

KIMURA, D. K.
1977. Statistical assessment of age-length key. J. Fish. Res. Board Can. 31:317-324.
1983. Determing appropriate sampling levels for estimating age distributions for trawl landings. Wash. Dep. Fish., Tech. Rep. 80, 18 p.

KUTKUHN, J. H.
1963. Estimating absolute age composition of California salmon landings. Calif. Fish Game, Fish. Bull. 120, 29 p.

LAI, H. L.
1985. Evaluation and validation of age determination of sablefish, pollock, Pacific cod and yellowfin sole; optimum sampling design using age-length key; and implications of aging variability in pollock. Ph.D. Thesis, Univ. Washington, Seattle, 426 p.

SCHWEIGERT, J. F., AND J. R. SIBERT.
1983. Optimizing survey design for determining age structure of fish stocks: an example from British Columbia Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 40:588-597.

SOUTHWARD, G. M.
1963. Sampling landings of halibut for age composition. Int. Pac. Halibut Comm. Sci. Rep. 58, 31 p.

TANAKA, S.
1953. Precision of age-composition of fish estimated by double sampling method using the length for stratification. Bull. Jpn. Soc. Sci. Fish. 19:657-670.

APPENDIX A. Derivation of Vartot

For a fixed age subsampling, substituting $n_j = n/L$ into Equation (2), the $\mathrm{Var}(p_i)$ is

$$\mathrm{Var}(p_i) = \sum_{j=1}^{L} \left[\frac{L\, l_j^2\, q_{ij}\,(1 - q_{ij})}{n} + \frac{l_j\,(q_{ij} - p_i)^2}{N} \right]. \qquad \text{(A.1)}$$

Applying Equation (3),

$$\mathrm{Vartot} = \sum_{i=1}^{A} \mathrm{Var}(p_i)$$

$$= \sum_{i=1}^{A} \sum_{j=1}^{L} \left[\frac{L\, l_j^2\, q_{ij}\,(1 - q_{ij})}{n} + \frac{l_j\,(q_{ij} - p_i)^2}{N} \right]$$

$$= \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [L\, l_j^2\, q_{ij}\,(1 - q_{ij})]}{n} + \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\,(q_{ij} - p_{ij})^2]}{N}$$

$$= \frac{a_1}{n} + \frac{a_2}{N}$$

which is Equation (4).

For a random age subsampling, substituting $n_j = n\, l_j$ into Equation (2) and applying Equation (3), the Vartot is

$$\mathrm{Vartot} = \sum_{i=1}^{A} \sum_{j=1}^{L} \left[\frac{l_j\, q_{ij}\,(1 - q_{ij})}{n} + \frac{l_j\,(q_{ij} - p_i)^2}{N} \right]$$

$$= \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\, q_{ij}\,(1 - q_{ij})]}{n} + \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\,(q_{ij} - p_i)^2]}{N}$$

$$= \frac{b_1}{n} + \frac{b_2}{N}$$

which is Equation (5).

APPENDIX B. Derivation of Equation (7)

The Cauchy-Schwarz inequality (Cochran 1977, p. 97) is

$$\left(\sum_h A_h^2\right)\left(\sum_h B_h^2\right) - \left(\sum_h A_h B_h\right)^2 = \sum_i \sum_{i>j} (A_i B_j - A_j B_i)^2 \geq 0. \quad \text{(B.1)}$$

Therefore,

$$\left(\sum_h A_h^2\right)\left(\sum_h B_h^2\right) \geq \left(\sum_h A_h B_h\right)^2.$$

For a fixed age subsample, let

$$A_1 = \sqrt{a_1/n};\ A_2 = \sqrt{a_2/N};\ B_1 = \sqrt{c_2 n};\ \text{and}\ B_2 = \sqrt{c_1 N}.$$

Applying Equation (B.1), the product of D^2 and C is

$$D^2 C = \left(\frac{a_1}{n} + \frac{a_2}{N}\right)(c_2 n + c_1 N) \geq \left(\sqrt{a_1 c_2} + \sqrt{a_2 c_1}\right)^2. \quad \text{(B.2)}$$

The product D^2C will be minimized, provided that the equality of Equation (B.2) holds. Setting equality of Equation (B.2) and expanding both sides, we find the solution is

$$r^* = (n/N)^* = \sqrt{a_1 c_1 / a_2 c_2} \quad \text{(B.3)}$$

which is Equation (7).

For a random age subsample, let

$$A_1 = \sqrt{b_1/n};\ A_2 = \sqrt{b_2/N};\ B_1 = \sqrt{c_2 n};\ \text{and}\ B_2 = \sqrt{c_1 N}.$$

The reader can derive Equation (11) by the procedures identical to Equations (B.2) and (B.3).

OOCYTE GROWTH AND DEVELOPMENT IN THE STRIPED MULLET, *MUGIL CEPHALUS*, DURING SEASONAL OVARIAN RECRUDESCENCE: RELATIONSHIP TO FECUNDITY AND SIZE AT MATURITY

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ABSTRACT

Oocyte growth and development in the striped mullet, *Mugil cephalus*, were examined during the period of rapid ovarian recrudescence that precedes spawning in coastal waters of northeast Florida. Based on the de novo appearance of yolk proteins detected by polyacrylamide gel electrophoresis, the oocyte size corresponding to the onset of vitellogenic growth was determined to be 0.18 mm (diameter). Through in vitro studies of oocyte responsiveness to steroid stimulation of meiotic maturation, the minimum prematuration oocyte size was determined to be 0.60 mm; largest prematuration oocytes collected during the study were 0.72 mm. Females with vitellogenic oocytes were first collected in Matanzas Inlet in late September. Females with prematurational oocytes were first observed in mid-October. Minimum size at sexual maturity for female striped mullet in northeast Florida ranged from 23 to 27 cm SL.

Oocyte size-frequency profiles led to the development of a staging system for striped mullet ovaries that can be related to simpler measurements of reproductive condition such as the gonadosomatic index and the largest oocyte diameter. According to this system, females with prespawning ovaries first appeared in Matanzas Inlet during mid-October, then disappeared from the Inlet in either mid-December (1985-86 season) or mid-January (1984-85 season). Females with ovaries in spawning condition were not observed in the Inlet during the 2 years of this study, supporting the commonly held assumption of offshore spawning. A few females with postspawn ovaries were collected as early as late November.

The potential fecundity of the striped mullet in northeast Florida was calculated from the size of the single clutch of developing oocytes, and related to both body weight and standard length.

The striped mullet, *Mugil cephalus*, is a euryhaline teleost with a nearly worldwide distribution in marine and estuarine waters. Economically important as a food and bait fish in many areas, the world commercial catch of mullet from 1979 to 1983 averaged nearly 185,000 t (metric tons) per year (FAO 1984). During this time, a yearly average of almost 14,000 t (nearly 8% of the world catch) were caught in the United States, more than in any other single country. Most were caught in the state of Florida, for an average of almost 12,000 t yearly in 1981 and 1982 (National Marine Fisheries Service preliminary data, in Comp and Seaman 1985), equivalent to 87% of the United States and 6% of the worldwide catch. In addition to being the basis of large natural fisheries, *M. cephalus* has been reared for aquacultural purposes in brackish and freshwater ponds (Bromhall 1954; Thomson 1966; Pien and Liao 1975) and has been the subject of induced breeding in the laboratory (Kuo et al. 1973, 1974a, b; Kuo 1982). General information on the biology of *M. cephalus* and related species of mullet can be found in Anderson (1958), Stenger (1959), and Thomson (1966).

Striped mullet have one breeding cycle per year lasting from 2 to 5 months depending on the location (Jacot 1920; Breder 1940; Bromhall 1954; Anderson 1958; Arnold and Thompson 1958; Stenger 1959; Tang 1964; Zhitenev et al. 1974; Pien and Liao 1975; Timoshek and Shilenkova 1975; Finucane et al. 1978; Apekin and Vilenskaya 1979; Azoury and Eckstein 1980; Chubb et al. 1981; Dindo and MacGregor 1981). In coastal waters of the southeast United States, spawning has been reported to occur from October through February as determined from the time of appearance and size of larvae and fry (Anderson 1958; Arnold and Thompson 1958), from the presence of migrating mullet with "developing" ovaries (Breder 1940; Arnold and Thompson 1958; Stenger 1959), and by monthly gonadosomatic index (GSI) changes (Dindo and MacGregor 1981).

In view of the extensive interest in the mullet, it

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is somewhat surprising that so little information concerning its reproduction, other than the seasonal spawning time, is available. For instance, little attention has been paid to the dynamics of oocyte development and ovarian recrudescence in natural striped mullet populations. A staging system for the ovary itself that would simply and meaningfully represent the extent of ovarian recrudescence in this species is lacking. And, although there have been numerous references to size of age at sexual maturity (Jacot 1920; Stenger 1959; Timoshek 1973; Apekin and Vilenskaya 1979), these are generally not based on comprehensive sampling. Similarly, although there have been equally numerous reports of striped mullet fecundity (Nash et al. 1973; Pien and Liao 1975; review by Alvarez-Lajonchere 1982), most derive from counts of eggs (or oocytes) in only a very limited number of fish, while body size-related data are virtually nonexistent.

We recently initiated several studies dealing with the reproduction of *M. cephalus* in coastal waters of northeast Florida and related topics. The specific purposes of this investigation include describing the patterns of oocyte growth during seasonal ovarian recrudescence, developing an ovarian staging system based on these patterns, and providing definitive determinations of both the size at maturity and the size-specific fecundity of female striped mullet in the area.

MATERIALS AND METHODS

Fish

Female striped mullet approximately 18 cm standard length (SL) or larger were captured by cast net from the Matanzas River Inlet south of St. Augustine, FL. Collections were made periodically from October 1984 through January 1985, and again from August 1985 through January 1986, for a total sample of 340 fish. Standard length and fork length (FL) were determined to the nearest 0.1 cm, and body weight (BW) to the nearest 0.1 g for all fish. Ovaries of most (248) fish ≥20 cm SL were removed and transferred to a buffered salt solution (FO: Wallace and Selman 1978), and any adhering non-ovarian tissue was removed. Whole ovaries were then patted dry and weighed to the nearest 0.01 g. The GSI for each fish was calculated as GSI = (ovary weight/body weight) × 100.

Oocyte Size-Frequency Profiles

Oocyte size-frequency profiles were constructed for each fish in the following manner. A representative (see below) piece was gently teased free from the middle of each newly collected ovary, patted dry, weighed to the nearest 0.1 mg, and placed in a petri dish containing FO solution. Pieces weighed from 1 to 9 mg and contained from 100 to 500 oocytes >0.10 mm in diameter. Individual follicle-enclosed oocytes were manually measured to the nearest 0.02 mm with an optical micrometer mounted on a dissecting microscope. Oocyte size-frequency profiles were not determined for fish with largest oocyte diameters (LODs) <0.10 mm, although their LODs were noted.

Profiles and LODs derived from a sample of ovary can be considered representative because oocyte development is known to occur uniformly throughout the mullet ovary (Ochiai and Umeda 1969; Shehadeh et al. 1973; Timoshek and Shilenkova 1975).

Oocyte Stages

The oocyte size at which vitellogenesis (the period of protein yolk accumulation) begins in the striped mullet was determined by the appearance of specific yolk protein bands in oocyte homogenates subjected to polyacrylamide gel electrophoresis (see Greeley et al. 1986b). Groups of small oocytes with mean diameters of 0.14, 0.16, 0.18, and 0.20 mm were isolated from surrounding ovarian tissue, homogenized in a sodium dodecyl sulfate (SDS) containing buffer solution, and heated at 100°C for 5 minutes. Samples were loaded onto a 0.75 mm thick polyacrylamide gradient gel (gradient: 3.5-20.4%) and were electrophoresed in SDS buffer with a constant applied current of 30 mAmps until the bromophenol blue marker migrated from the gel. Protein fixation, visualization with Coomassie blue, and molecular weight determinations were conducted as in Wallace and Selman (1985). Biochemicals and reagents were highest available grades from Sigma Chemical Company[3] and Bio-Rad Laboratories.

The minimum oocyte size competent to resume meiotic maturation (leading to the development of a mature fertilizable egg) in response to steroid hormone stimulation was determined in vitro by the methods of Greeley et al. (1986a). Larger follicle-enclosed oocytes were isolated in FO and assigned to one of four pools with mean diameters of 0.52, 0.56, 0.60, and 0.64 mm. Oocytes from each pool were randomly subdivided into treatment (steroid

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

added) and control groups, and then transferred into separate 35 × 10 mm petri dishes containing 3 mL of a 75% L-15 culture medium (Sigma) at pH 7.5. A solution containing 3 μg of 17α-hydroxy-20β-dihydroprogesterone in 10 μL of 95% ethanol was added to each treatment dish (for a final steroid concentration of 1 μg/mL); 10 μL of 95% ethanol was added to each control dish. Oocytes were incubated at 20°C for 48 hours and then examined for germinal vesicle breakdown (GVBD), which was easily noted by the absence of the germinal vesicle (GV) or nucleus in the highly transparent postmaturation oocyte, as an indicator of the resumption of meiotic maturation in response to the hormone.

Fecundity

Potential fecundity was estimated for each fish whose oocyte size-frequency profile demonstrated that recruitment of oocytes into vitellogenesis had ceased as potential fecundity = [(number of recruited oocytes in ovary piece) × (weight of whole ovary)]/(piece weight).

RESULTS

Gonadosomatic Index (GSI)

Ovarian recrudescence in the striped mullet occurs during autumn and early winter in coastal waters of northeast Florida, as indicated by seasonal changes in the GSIs of females collected from the Matanzas River Inlet (hereafter referred as Inlet) during the 1984-85 and 1985-86 breeding seasons (Fig. 1). In August of 1985, the earliest month of collections for this study, GSIs were <1 in all sampled fish. Ovaries represented by these low GSIs were quite small and were either translucent and colorless (smallest and least developed ovaries) or opaque with a red hue resulting from extensive vascularization (slightly larger and more developed ovaries). Similar low GSIs continued to be found in all females collected through mid-September.

In late September the GSIs of a portion of the collected females rose sharply, to nearly 9. The much larger ovaries represented by these high GSIs were

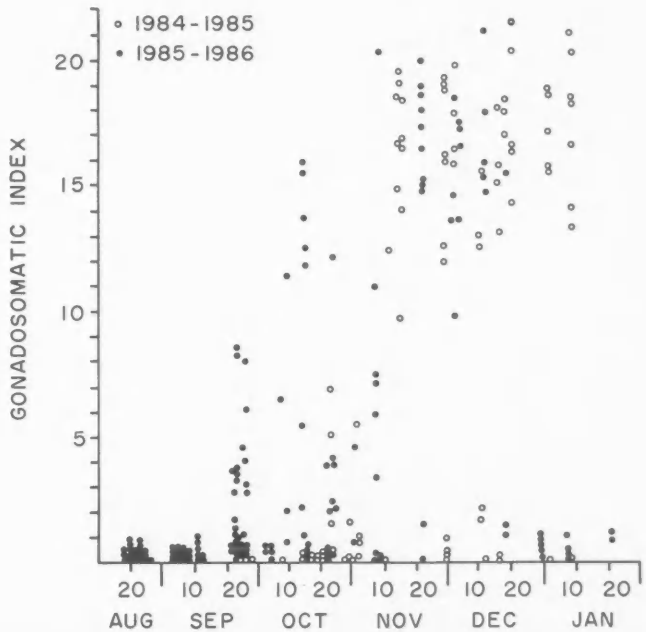

FIGURE 1.—Variation in the gonadosomatic index (GSI) of female *Mugil cephalus* ≥20 cm SL during prespawning ovarian recrudescence along the northeast Florida coast.

now yellow to golden in color because of a preponderance of yellow yolky oocytes in the ovarian lamellae. This initial phase of GSI increases continued through early November, at which time two distinct groupings of females within the population became apparent: those with GSIs remaining <2, and those with GSIs ranging between 10 and 21. Average GSIs in the latter group rose only slightly thereafter, ranging from 13 to 22 by early December. The lower GSIs of the rest of the population remained unchanged throughout the remainder of this study.

During the 1984-85 season, females with high GSIs continued to be caught until mid-January, at which time larger females (≥20 cm SL) apparently left the Inlet because none were caught during the 3 additional weeks of intensive collecting. In contrast, during the 1985-86 season, females with high GSIs were only collected through mid-December. Although a few mid-size females were collected through late January of this year after the expenditure of considerable collecting time and effort, all proved to have small GSIs.

Oocyte Stages

A primary purpose of this project was to document the oocyte growth and development that accompanied these GSI changes during prespawning ovarian recrudescence. Two oocyte development stages of primary interest to us were 1) the stage at which yolk accumulation or vitellogenesis begins, and 2) the stage during, or following, vitellogenic growth when the oocyte first becomes competent to resume meiotic maturation and thereby develop into a fertilizable egg.

We previously showed two large proteins at M_r = 104,000 and 90,000 to be the major yolk proteins present in mullet oocytes at the end of vitellogenic growth (Greeley et al. 1986b). As evidenced by the de novo appearance of these marker proteins (Fig. 2), vitellogenesis in the striped mullet begins in oocytes that are between 0.16 and 0.18 mm in diameter. In this study, oocytes 0.16 mm in diameter and smaller are thus considered to be previtellogenic, a broad classification including both primary growth- and yolk vesicle-stage oocytes as described

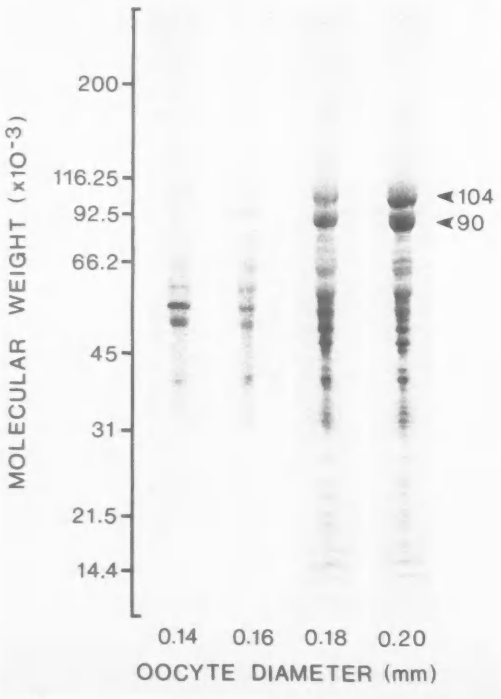

FIGURE 2.—Polyacrylamide gel electrophoresis of oocyte proteins indicating de novo appearance of yolk proteins in vitellogenic oocytes (0.18 mm in diameter) of the *Mugil cephalus*, with comparison to smaller previtellogenic and larger vitellogenic oocytes (see text). Molecular weight standards are indicated on the left for comparison; the molecular weights of the two major yolk proteins are shown on the right (arrows).

by Wallace and Selman (1981); oocytes 0.18 mm in diameter and larger are considered to be actively vitellogenic.

Late vitellogenic oocytes become competent to resume meiotic maturation and develop into a fertilizable egg in response to an in vitro steroid challenge at 0.60 mm in diameter, with larger oocytes being only marginally more responsive (Table 1). Therefore, oocytes 0.60 mm and larger that do not exhibit any signs of maturation such as yolk "clearing" or hydration are considered to be in a prematuration stage of development.

Striped mullet eggs following meiotic maturation are even larger (0.90 to 1.00 mm in diameter) (Abraham et al. 1966; Nash et al. 1973; Pien and Liao 1975; Finucane et al. 1978; Greeley et al. 1986b), nearly transparent (yolk has cleared), hydrated, float in full-strength seawater, and thus are easily distinguished from the smaller and more opaque prematuration oocytes. Females with mature eggs were not collected during this study.

TABLE 1.—Percentage of different-sized striped mullet oocytes undergoing germinal vesicle breakdown (GVBD) in vitro in response to treatment with 17α-hydroxy-20β-dihydroprogesterone (1 μg/mL) or an ethanol control.

Oocyte diameter (mm)	Treatment	*N*	(%)GVBD
0.52	control	55	0
	steroid	50	0
0.56	control	50	0
	steroid	45	0
0.60	control	326	0
	steroid	301	65
0.64	control	196	0
	steroid	198	71

Largest Oocyte Diameter (LOD)

The relationship of oocyte diameter to stages of oocyte development is clearly delineated in Figure 3. Three major developmental stages are shown: 1) previtellogenic growth, including both the pri-

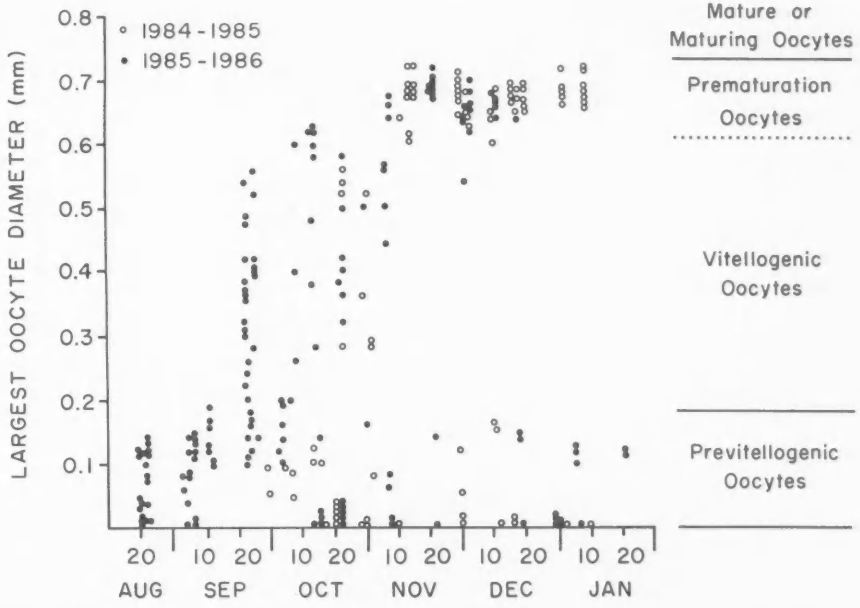

FIGURE 3.—Variation in the largest oocyte diameter (LOD) of female *Mugil cephalus* ≥20 cm SL during prespawning ovarian recrudescence along the northeast Florida coast. Presented on the right are oocyte developmental stages corresponding to these oocyte sizes. Broken line between vitellogenic and prematuration designations signifies uncertainty concerning whether the latter is actually a substage of the former. The category "previtellogenic" encompasses both primary growth and yolk vesicle oocytes.

mary growth and yolk vesicle phases as defined by Wallace and Selman (1981), 2) vitellogenic growth, and 3) maturation. An additional developmental category—prematuration—may or may not be considered a substage of late vitellogenesis; although oocyte growth appears to level off at this time, we have no direct evidence that the oocyte completely ceases to take up yolk precursors at this time.

Changes in the LOD (Fig. 3) during the period of seasonal ovarian recrudescence were similar to changes in the GSI. LODs were small in August and early September, representative of still previtellogenic oocytes. LODs then rose sharply in mid-September as vitellogenic oocytes began to appear in females captured in the Inlet. The range of LODs in the population at this time varied considerably, from <0.01 mm in some fish to nearly 0.56 mm in others. LODs continued to rise in one portion of the population through mid-November, before leveling off between 0.60 and 0.72 mm; in other females, LODs remained below 0.18 mm through the end of each study period. Females with high LODs were last collected in mid-December during the 1985-86 breeding season and in mid-January during the 1984-85 season.

Body Size at Maturity

An examination of the LODs as a function of standard length on a month to month basis (Fig. 4) reveals several body size-related trends that bear on the results presented in Figure 3. During August, the first month of the collections, there was little difference between the LODs of different-sized females, all being low and representative of previtellogenic oocytes. Only a few large striped mullet were collected during this month. This changed in September, with larger females over 32 cm SL becoming more prevalent in the Inlet and exhibiting a tendency to have higher LODs than smaller females. By October, smaller females (to a lower limit of 28 cm SL) also began to acquire vitellogenic oocytes, although their average LODs were still lower than those of larger females. During November, LODs of larger females leveled off at 0.60 to 0.72 mm, but a few smaller females (now to a lower limit of 26 cm SL) continued to have intermediate LODs indicative of oocytes in the early stages of vitellogenesis. By December and January, recruitment of smaller females into sexual maturity apparently ceased because LODs were now uniform—either greater than the 0.60 mm prematurational oocyte size or less than the minimum 0.18 mm vitellogenic size—in all females regardless of body size.

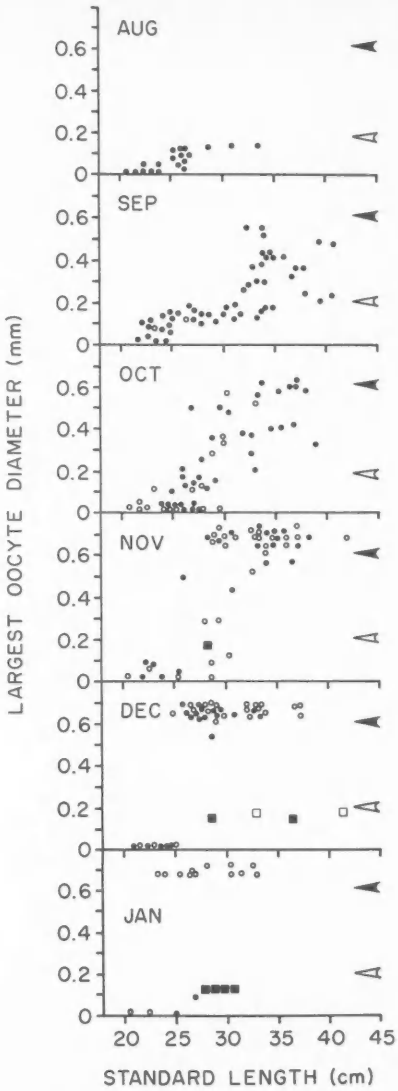

FIGURE 4.—Monthly variation in the relationship of the largest oocyte diameter (LOD) to standard length (SL) in female *Mugil cephalus* during prespawning ovarian recrudescence along the northeast Florida coast. Circles represent data points from prespawning females (open: 1984-85; closed 1985-86); squares represent data points from postspawn females (open: 1984-85; closed 1985-86). Open arrows indicate oocyte size at beginning of vitellogenesis; solid arrows indicate minimum prematuration oocyte size.

During November, December, and January, a few larger females with LODs less than the minimum 0.18 mm vitellogenic size were collected from the Inlet. This suggested that seasonal ovarian recrudescence does not occur in all large females every year. However, other criteria (see below) indicated that these were actually postspawn ovaries.

Minimum female size at maturity by the end of the season ranged from 23 to nearly 27 cm SL. Three size-categories of females can now be recognized: 1) those smaller than 23 cm SL that are obligatory immatures; 2) those 23 to 27 cm SL that may enter into maturity before the end of the spawning season; and 3) those larger than 27 cm SL that are always sexually mature sometime during the spawning season. The minimum body size at sexual maturity can also be expressed as a function of fork length (27 to 31 cm) or body weight (232 to 383 g) with the use of the equations provided in Figure 5.

Ovary Stages

LODs are useful criteria for following the course of ovarian recrudescence in the striped mullet and for determining the size or age of females at sexual maturity. Yet the LOD by itself cannot distinguish between sexually immature and postspawn females,

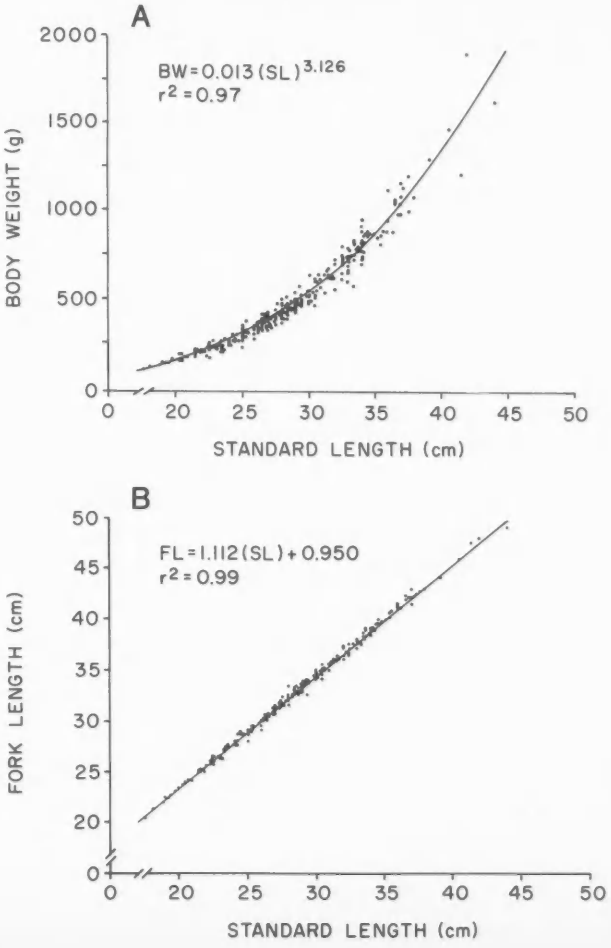

FIGURE 5.—Relationship of (A) body weight and (B) fork length to the standard length of female *Mugil cephalus* (≥20 cm SL) during prespawning ovarian recrudescence along the northeast Florida coast. Lines were fitted by least squares regression.

nor does it provide information about the range of oocyte sizes to be found in individuals. To better understand the pattern of oocyte development leading to the formation of a clutch of mature eggs, it is necessary to examine comprehensive oocyte size-frequency profiles. Representative profiles of Figure 6 illustrate both the pattern of oocyte development during ovarian recrudescence in the striped mullet and an ovarian staging system based upon these profiles.

In ovarian stage I (previtellogenesis), yolk accumulation by developing oocytes has not yet begun, as all oocytes are less than the minimum previtellogenic size of 0.18 mm in diameter. An oocyte size-

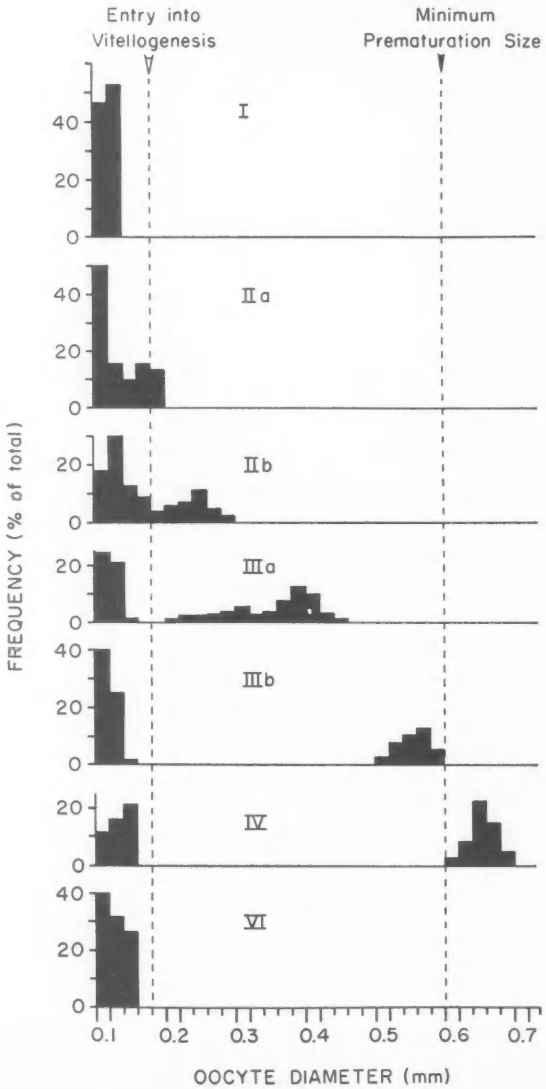

FIGURE 6.—Representative oocyte size-frequency profiles corresponding to stages of ovarian recrudescence in *Mugil cephalus*. Dashed line on left represents the transition between previtellogenic and vitellogenic oocytes; dashed line on the right delineates the minimum prematuration oocyte size. See text for explanation of stages.

frequency profile from an ovary in this stage is shown in Figure 6. GSIs of females with stage I ovaries ranged up to 0.8.

Stage II (early vitellogenesis) is characterized by recruitment of previtellogenic oocytes into vitellogenesis. A single clutch of vitellogenic oocytes starts to form, becoming distinct from the remaining mass of previtellogenic oocytes as the recruited oocytes increase in diameter due to yolk accumulation. This stage can be further divided into two substages on the basis of the appearance of the profiles. In stage IIa, recruitment into vitellogenesis has just begun; a clear separation between the developing (vitellogenic) and nondeveloping (previtellogenic) oocytes is not yet discernible. In stage IIb, the developing clutch forms a distinct peak (or peaks) as recruitment and subsequent vitellogenic growth continues. LODs of females with stage II ranged from 0.18 to 0.56 mm; GSIs varied from 0.3 to 8.5.

In stage III (mid- to late-vitellogenesis), recruitment into vitellogenesis ceases, although oocytes in the recruited clutch continue to increase in diameter due to further yolk accumulation. This stage can also be divided into two substages. In stage IIIa, recruitment has just ended: the recruited clutch is spread out in size, and multiple size-frequency peaks are apparent. In stage IIIb, the recruited clutch tightens into a single peak; oocyte diameters continue to increase. LODs of females with stage III ovaries varied from 0.40 to 0.59 mm; GSIs ranged from 2.1 to 12.1.

In stage IV (prespawning), oocytes in the recruited clutch reach the minimum prematuration size of 0.60 mm in diameter and become capable of resuming maturation in response to a hormonal signal. Late in the stage, as shown in Figure 6, all oocytes in an ovary will be at, or above, the minimum prematuration size. LODs of females with stage IV ovaries were 0.60 and 0.72 mm; GSIs were more scattered, from a low of 11.4 to a high of 21.2.

Stage V (spawning: not shown) is characterized by the presence in the ovary of maturing oocytes or mature eggs. No fish with ovaries in this stage were caught in the Inlet; however, this stage was produced in the laboratory by injection of human chorionic gonadotropin into prespawning females (Greeley et al. 1986b).

Stage VI (postspawn) ovaries, upon gross examination, are small, red, and flaccid in appearance with a thickened ovarian wall. Spawning is apparently complete—at least by the time the females return to the Inlet—as no partially spawned ovaries were collected, nor were large atretic oocytes or eggs ever observed. LODs of postspawn females were 0.12 to 0.14 mm; GSIs ranged from 0.1 to 1.6.

Monthly changes in the relative frequency of these stages in females collected from Matanzas Inlet during ovarian recrudescence in 1985-86 are shown in Figure 7. The variation in these stages is similar to the variation observed in the LOD, although the ovarian stages provide a somewhat different infor-

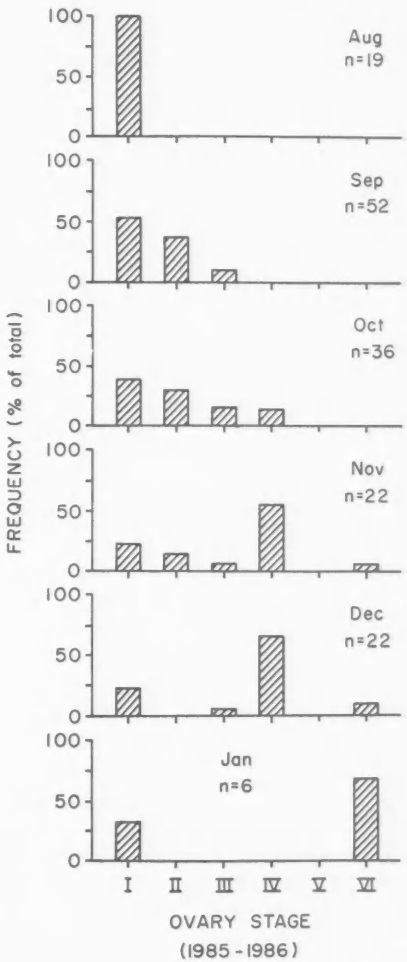

FIGURE 7.—Monthly variation in ovarian stages of adult *Mugil cephalus* (≥20 cm SL) during prespawning ovarian recrudescence along the northeast Florida coast. Data presented for the 1985-86 season only (see text).

mation. In August, only fish with previtellogenic ovaries (stage I) were collected. During September and October, a variety of ovary stages were observed, from previtellogenic (stage I) to prespawning (stage IV). Ovaries with active recruitment of oocytes into vitellogenesis (stages IIa and b) were not observed after October. The first postspawn fish (stage VI) was caught in late November, and by January only previtellogenic or postspawn fish were caught. Variation in ovary stages during the 1984-85 season (not shown) was similar, except that in this year females with prespawning (stage IV) ovaries were collected as late as mid-January.

Fecundity

Because oocyte size-frequency profiles indicate that only a single clutch of developing oocytes proceeds through vitellogenesis in a season, and that this single clutch is eventually spawned in its entirety, it is possible to calculate the individual fecundity of a female striped mullet by counting the number of vitellogenic oocytes in stages IIIa-IV ovaries (in which recruitment of oocytes into developing clutches has ceased). The annual potential fecundity, or number of eggs available to be spawned in a single breeding season, was thus found to be linearly related to body weight and geometrically related to standard length (Fig. 8). The lowest fecundity observed was 0.25×10^6 eggs in a fish 264 g BW and 23.5 cm SL, and the highest fecundity was 2.2×10^6 eggs in a fish 1,627 g BW and 44 cm SL.

DISCUSSION

The present results indirectly confirm that the spawning season of *M. cephalus* in coastal waters of northeast Florida extends from at least late November (when the first postspawn female was collected during the 1985-86 season) through mid-January (when the last prespawn female was collected during the 1984-85 season). However, there is probably a certain amount of year-to-year variation within this range: the first postspawn female was not observed until December during one season (1984-85), while the last prespawn in another (1985-86) was collected in December rather than January.

It is also probable that these dates are in reality only a conservative estimate of the actual range of the striped mullet spawning season in this area. Available evidence from other studies strongly suggest that striped mullet spawn offshore (Anderson 1958; Arnold and Thompson 1958; Finucane et al. 1978). If this is also true of striped mullet in northeast Florida, then postspawn females collected in November may have traveled extensively between spawning at offshore sites and their eventual capture in the Inlet. Likewise, the prespawn females collected in January would have required some time to reach offshore spawning sites after leaving the Inlet. Therefore, adding a month to each end of the observed range to conservatively account for such migrations may be appropriate and would make our dates consistent with previously published reports of spawning times for striped mullet in the southeast United States ranging from October through February (Broadhead 1956; Anderson 1958; Dindo and MacGregor 1981).

Do striped mullet of northeast Florida actually spawn offshore? The best evidence for offshore spawning migrations in this study was our failure to collect from the Inlet any females with spawning ovaries or even partially spent ovaries, suggesting that spawning probably occurred some distance from the Inlet. Further evidence for an offshore spawning site were the abrupt disappearances from the Inlet of fish with prespawning ovaries during both years of the study (mid-January 1984-85 and mid-December 1985-86), as this behavior suggested that mass spawning migrations to offshore waters occurred at these times.

If these disappearances did represent mass offshore spawning migrations, then how can we explain the earlier appearances in the Inlet of a few postspawn fish? Perhaps there are actually multiple spawning migrations, possibly by different populations of striped mullet moving through the Inlet at intervals throughout the period. Or perhaps some inshore spawning also occurs: staff at the Whitney Laboratory[4] have occasionally observed what they considered to be striped mullet spawning activity in the Intracoastal Waterway near the Inlet, and there are a few anecdotal accounts of inshore spawning in the literature (Breder 1940; Gunter 1945; Timoshek and Shilenkova 1975). However, if inshore spawning does occur, it must be limited in scope; otherwise, we would have collected females with spawning ovaries in the Inlet during our own studies. It may be that striped mullet can spawn either inshore or offshore, with offshore spawning favored, depending on factors—such as salinity, temperature, winds, currents, tides, or some combination thereof—which vary from locale to locale and from year to year.

[4]W. Raulerson, Whitney Laboratory, University of Florida, Route 1, Box 121, St. Augustine, FL 32086, pers. commun.

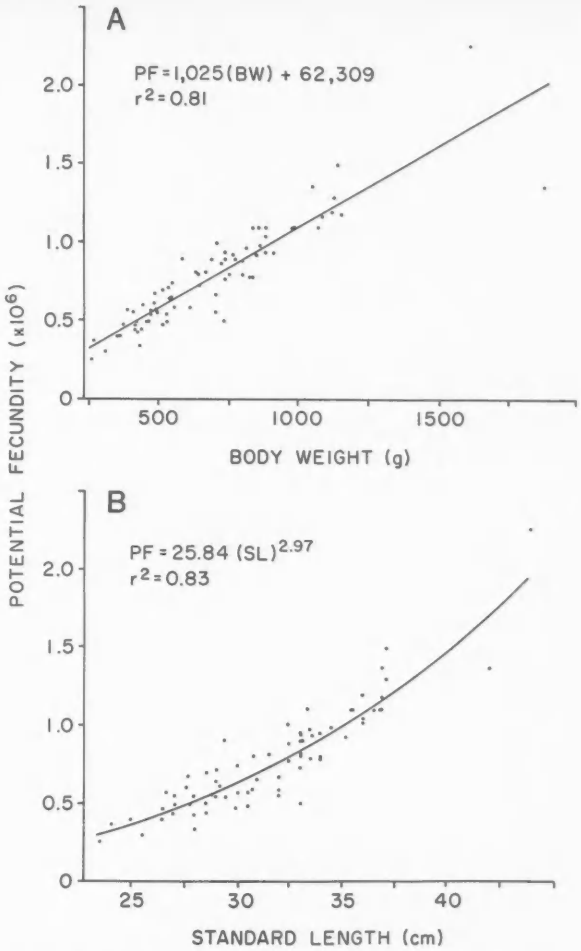

FIGURE 8.—The relationship of the potential annual fecundity of *Mugil cephalus* from northeast Florida to (A) body weight and (B) standard length. Lines are drawn from regression equations.

In fact, the apparent timing of the hypothetical final spawning migrations from the Inlet in each of the two seasons of the present study suggests there might be a tidal involvement in these events: one coincided with a set of new moon spring tides, and the other to a set of full moon spring tides. Such a tidal or lunar connection to spawning migrations of striped mullet has been proposed previously (Bromhall 1954), although supporting evidence is still inconclusive. Others have alternatively suggested wind and currents might be contributing factors to the onset of spawning migrations (Apekin and Vilenskaya 1979); further work is needed to clarify these issues.

Most workers agree that individual female *M. cephalus* spawn only once a year (Zhitenev et al. 1974; Timoshek and Shilenkova 1975; Chubb et al. 1981). Our results support this assumption, as we never observed more than a single clutch of developing oocytes proceeding through vitellogenesis dur-

ing the fall period of prespawning ovarian recrudescence. Our failure to collect any partially spawned females is also consistent with a single seasonal spawn.

In this study, both the GSI and the LOD proved to be adequate, although not completely satisfactory, indicators of the reproductive condition of female striped mullet. However, of these two indices the LOD would appear to be preferable. Determination of the LOD requires only the biopsy of a small piece of ovary (see Shehadeh et al. 1973) which can be easily accomplished without harm to the fish, while determination of the GSI requires the sacrifice of the fish. Furthermore, the validity of the GSI has been questioned (deVlaming et al. 1982) as to its accuracy in correcting for body size in a consistent manner over all reproductive stages.

On the other hand, the speed and ease of obtaining the LOD are its only advantages over a more comprehensive indicator of reproductive condition —the oocyte size-frequency profile. Such a profile also requires only the biopsy of a small piece of ovary and is a much more accurate indicator of ovarian stage, especially during the active vitellogenic growth of the ovary when a developing clutch may be quite spread-out in size.

An adequate understanding of the functional relationship between oocyte size and stage is, of course, required for correct interpretation of either LODs or oocyte size-frequency profiles. Of particular interest to us during this study were the sizes of the oocyte at 1) the beginning of vitellogenesis and 2) the prematuration stage of development. Our data indicate that oocytes of the striped mullet are able to grow to a point immediately prior to vitellogenic growth, then temporarily arrest at that stage. In contrast, once vitellogenic growth begins, further development leading to a subsequent clutch of mature eggs is apparently ensured. Thus knowledge of this transition point is extremely important to investigators attempting to predict the future reproductive status of these fish. Likewise, clearly identifying the prematuration stage of oocyte is important because at this stage the oocyte is competent to resume meiotic maturation culminating in the formation of a fertilizable egg.

We define the beginning of vitellogenesis in the striped mullet oocyte by the initial appearance of yolk proteins detectable by electrophoretic techniques and the prematuration stage of development by in vitro culture techniques. Our resulting prematuration stage is in essential agreement with the "functional maturity" stage of Kuo et al. (1974b), as is our 0.18 mm initial vitellogenic stage with the initial "yolk globule" stage (0.20 mm) of these authors. We did not examine smaller oocytes in detail and thus did not attempt to establish specific stages for previtellogenic oocytes.

The oocyte size-frequency profiles of this study, plus the additional data relating oocyte sizes and stages, demonstrate that *M. cephalus* has a group-synchronous type of oocyte development, as originally defined by Marza (1938) and reiterated by Wallace and Selman (1981). In such an ovary, a single developing clutch of oocytes coexists with an apparently asynchronous pool of previtellogenic oocytes. However, it must be pointed out that in the mullet this pattern is not always straightforward. The movement of oocytes into vitellogenesis is quite prolonged in time, so that a truly discrete clutch, as characterized by the cessation of additional recruitment into the clutch, does not become apparent until the more developed oocytes within the clutch are already well into vitellogenic growth. Furthermore, even after recruitment into vitellogenesis ceases, the developing clutch can be quite heterogenous in size (see oocyte size-frequency profile for ovarian stage IIIa, Figure 6) and thus may not appear to be undergoing synchronous growth until ovarian stage IIIb. Such a pattern of oocyte development could be very difficult to characterize without examination of ovaries from females collected throughout the period of ovarian recrudescence.

To the best of our knowledge, the ovary staging system put forth in this paper is the only such comprehensive system developed specifically for the striped mullet. Based on well-defined and physiologically significant criteria, it is presented with the purpose of standardizing future studies dealing with reproduction in the striped mullet.

The range (23 to 27 cm SL) we present for the size at maturity of striped mullet in northeast Florida is similar to the only other published report for the area (25 cm SL by Stenger 1959), but much lower than the values (30 to 46 cm SL) reported by Jacot (1920), Thomson (1951), Ochiai and Umeda (1969), Timoshek (1973), and Apekin and Vilenskaya (1979). Most investigators agree that female mullet reach sexual maturity at the end of their third year (Thomson 1951; Timoshek 1973). We made no attempt to age the fish because methods available were not always agreed upon (see Thomson 1966). However, according to the growth schedules of Thomson (1966), adapted from various primary sources, the age at maturity in this study apparently ranged from 2¼ years (23 cm SL) to 2½ years (27 cm SL).

It thus appears that female *M. cephalus* attain sex-

ual maturity in northeast Florida at a smaller size, and probably at an earlier age, than anywhere else in the world. However, caution must be taken in making such comparisons. Our results demonstrate that smaller fish typically lag behind larger fish in reaching a sexually developed state by as much as 2 months on a seasonal basis. In consequence, the determinations of size or age at maturity by other investigators, if based on only a limited number of samples or on samples obtained at only a limited number of dates within the prespawning period of ovarian recrudescence, might not be truly comparable to our results.

The annual fecundity of *M. cephalus* has been reported to be from 1.2×10^6 to 2.8×10^6 by most authors (Thomson 1966), although estimates ranged from as low as 0.5×10^6 to as high as 14×10^6 (from review by Alvarez-Lajonchere 1982). Unfortunately, the methods whereby these values were obtained are often not given, so many reports have to be considered suspect. In addition, data concerning size-related trends in the fecundity of striped mullet are nearly nonexistent. By contrast, our estimates of fecundity (0.25×10^6 to 2.5×10^6) are well-documented and demonstrate a clear and highly predictable relationship between individual fecundity and body size.

In conclusion, this study describes the pattern of oocyte development during seasonal ovarian recrudescence in the striped mullet, proposes an ovarian staging system based on oocyte stages and size-frequency profiles, gives a range of values for the female size at maturity, and presents the only comprehensive examination of size-related fecundity for *M. cephalus* to date.

ACKNOWLEDGMENTS

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LITERATURE CITED

ABRAHAM, M., N. BLANC, AND A. YASHOUV.
1966. Oogenesis in five species of grey mullets (Teleostei, Mugilidae) from natural and landlocked habitats. Isr. J. Zool. 15:155-172.

ALVAREZ-LAJONCHERE, L.
1982. The fecundity of mullet (Pisces, Mugilidae) from Cuban waters. J. Fish Biol. 21:607-613.

ANDERSON, W. W.
1958. Larval development, growth, and spawning of striped mullet (*Mugil cephalus*) along the south Atlantic coast of the United States. U.S. Fish. Wildl. Serv., Fish Bull. 58:501-519.

APEKIN, V. S., AND N. I. VILENSKAYA.
1979. A description of the sexual cycle and the state of the gonads during the spawning migration of the striped mullet, *Mugil cephalus*. J. Ichthyol. 18:446-456.

ARNOLD, E. L., AND J. R. THOMPSON.
1958. Offshore spawning of the striped mullet, *Mugil cephalus*, in the Gulf of Mexico. Copeia 1958:130-132.

AZOURY, R., AND B. ECKSTEIN.
1980. Steroid production in the ovary of the gray mullet *Mugil cephalus* during stages of egg ripening. Gen. Comp. Endocrinol. 42:244-250.

BREDER, C. M.
1940. The spawning of *Mugil cephalus* on the Florida west coast. Copeia 1940:138-139.

BROADHEAD, G. C.
1956. Growth of the black mullet *Mugil cephalus* in west and northwest Florida. Fla. Board Conserv. Mar. Lab. Tech. Ser. 25:1-29.

BROMHALL, J. D.
1954. A note on the reproduction of the grey mullet, *Mugil cephalus* Linnaeus. Hong Kong Univ. Fish. J. 1:19-34.

CHUBB, C. F., I. C. POTTER, C. J. GRANT, R. C. J. LENANTON, AND J. WALLACE.
1981. Age, structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon river system, western Australia. Aust. J. Mar. Freshw. Res. 32:605-628.

COMP, G. S., AND W. SEAMAN, JR.
1985. Estuarine habitat and fishery resources of Florida. *In* S. Seaman, Jr. (editor), Florida aquatic habitat and fishery resources, p. 337-435. Florida Chapter of American Fisheries Society, Kissimmee, FL.

DEVLAMING, V., G. GROSSMAN, AND F. CHAPMAN.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31-39.

DINDO, J. J., AND R. MACGREGOR III.
1981. Annual cycle of serum gonadal steroids and serum lipids in striped mullet. Trans. Am. Fish. Soc. 110:403-409.

FAO.
1984. 1983 yearbood of fisheries statistics. Catches and landings. Vol. 56. Rome, Italy.

FINUCANE, J. H., L. A. COLLINS, AND L. E. BARGER.
1978. Spawning of the striped mullet, *Mugil cephalus*, in the northwestern Gulf of Mexico. Northeast Gulf Sci. 2:148-150.

GREELEY, M. S., JR., D. R. CALDER, M. H. TAYLOR, H. HOLS, AND R. A. WALLACE.
1986a. Oocyte maturation in the mummichog (*Fundulus heteroclitus*): Effects of steroids on germinal vesicle breakdown of intact follicles *in vitro*. Gen. Comp. Endocrinol. 62:281-289.

GREELEY, M. S., JR., D. R. CALDER, AND R. A. WALLACE.
1986b. Changes in teleost yolk proteins during oocyte maturation: Correlation of yolk proteolysis with oocyte hydration. Comp. Biochem. Physiol. 84B:1-9.

GUNTER, G.
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. Univ. Texas 1:1-194.

JACOT, A. P.
1920. Age, growth, and scale characters of the mullets: *Mugil cephalus* and *Mugil curema*. Trans. Am. Microsc. Soc. 39: 199-299.

KUO, C.-M.
1982. Induced breeding of grey mullet, *Mugil cephalus* L.

In C. J. J. Richter and H. J. Th. Goos (editors), Reproductive physiology of fish, p. 181-184. Pudoc, Wageningen.

KUO, C.-M., Z. H. SHEHADEH, AND C. E. NASH.
1973. Induced spawning of captive grey mullet (*Mugil cephalus* L.) females by injection of human chorionic gonadotropin (HCG). Aquaculture 1:429-432.

KUO, C.-M., C. E. NASH, AND Z. H. SHEHADEH.
1974a. A procedural guide to induce spawning in grey mullet (*Mugil cephalus* L.). Aquaculture 3:1-14.
1974b. The effects of temperature and photoperiod on ovarian development in captive grey mullet (*Mugil cephalus* L.). Aquaculture 3:25-43.

MARZA, V. D.
1938. Histophysiologie de 1a ovogenese. Hermann, Paris, 81 p.

NASH, C. E., C.-M. KUO, AND S. C. MCCONNELL.
1973. Operational procedures for rearing. *In* The grey mullet: Induced breeding and larval rearing 1972-1973, Vol. II, p. 23-34. Oceanic Inst. Tech. Rep. 01-73-128.

OCHIAI, A., AND S. UMEDA.
1969. Spawning aspects of the grey mullet, *Mugil cephalus* L., living on the coastal region of Kochi Prefecture. [In Jpn, Engl. summ.]. Jpn. J. Ichthyol. 16:50-54.

PIEN, P.-C., AND I.-C. LIAO.
1975. Preliminary report of histological studies on the grey mullet gonad related to hormone treatment. Aquaculture 5:31-39.

SHEHADEH, Z. H., C.-M. KUO, AND K. K. MILISEN.
1973. Validation of an *in vivo* method for monitoring ovarian development in the grey mullet (*Mugil cephalus* L.). J. Fish Biol. 5:489-496.

STENGER, A. H.
1959. A study of the structure and development of certain reproductive tissues of *Mugil cephalus* Linnaeus. Zoologica, N.Y. 44:53-70.

TANG, Y. A.
1964. Induced spawning of striped mullet by hormone injection. [In Jpn., Engl. summ.] Jpn. J. Ichthyol. 12:23-28.

THOMSON, J. M.
1951. Growth and habits of the sea mullet, *Mugil dobula* Gunther, in western Australia. Aust. J. Mar. Freshw. Res. 2: 193-225.
1966. The grey mullets. Oceanogr. Mar. Biol. Ann. Rev. 4: 301-335.

TIMOSHEK, N. G.
1973. The distribution and migration of mullet in the Black Sea. [In Russ., Engl. summ.] Tr. Vses. Naucho-Issled. Inst. Morsk. Rybn. Khoz. 93:163-177.

TIMOSHEK, N. G., AND A. K. SHILENKOVA.
1975. The nature of the oogenesis and spawning of Black Sea mullet. J. Ichthyol. 14:727-746.

WALLACE, R. A., AND K. SELMAN.
1978. Oogenesis in *Fundulus heteroclitus* I. Preliminary observations on oocyte maturation *in vivo* and *in vitro*. Dev. Biol. 62:354-369.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325-343.
1985. Major protein changes during vitellogenesis and maturation of *Fundulus* oocytes. Dev. Biol. 110:492-498.

ZHITENEV, A. N., D. S. KALININ, AND Y. I. ABEYEV.
1974. The state of the gonads of the striped mullet (*Mugil cephalus*) and the sharpnose mullet (*Mugil saliens*) leaving estuaries to spawn, and their reaction to a pituitary injection. J. Ichthyol. 14:232-239.

DEVELOPMENT OF THE EGGS AND LARVAE OF THE YELLOWCHIN SCULPIN, *ICELINUS QUADRISERIATUS* (PISCES: COTTIDAE)

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ABSTRACT

The development of the eggs and larvae of *Icelinus quadriseriatus* is described from laboratory-reared and field-collected specimens.

The eggs have diameters from 1.08 to 1.17 mm, an adhesive chorion, and multiple oil globules. Before hatching the oil globules coalesce into one 0.14-0.19 mm in diameter. The embryo develops a patch of tubercles on the dorsal surface of the head that are lost immediately after hatching.

The larvae hatch at 2.6-3.4 mm. Distinguishing characters are 1-6 rows of ventral gut melanophores, 25-63 postanal ventral melanophores, and lower jaw angle pigment. Larvae over 3.9 mm may develop chin and pectoral insertion melanophores. Nasal and parietal spines appear at 9.3 mm. Postflexion larvae develop three patches of pigment dorsolaterally on the body by 10.5 mm and transform to juveniles by 16.3 mm.

Scorpaeniform fishes are represented in the North Pacific Ocean by a large group of endemic taxa whose early life histories are poorly known. The early life histories of many sculpins (Cottidae), the second largest family in the order, were recently described (Richardson and Washington 1980). Larvae of several species of *Artedius*, *Clinocottus*, and *Oligocottus* have been described by Washington (1986). *Synchirus gilli* larvae were described by Marliave et al. (1985). Reared and field-collected larvae of *Chitonotus pugetensis* have been described (Misitano 1980; Richardson and Washington 1980); however, the larval stages of the closely related *Icelinus*, including nine described species and one undescribed species (Yabe et al. 1980; R. Rosenblatt[2]), are unknown. The purpose of this paper is to describe the eggs and larvae of the yellowchin sculpin, *Icelinus quadriseriatus*, using both laboratory-reared and field-collected material.

Icelinus quadriseriatus occurs along the coast of California north to Sonoma County (lat. 38°23.5′N; long. 123°08′W) and south to Cabo San Lucas, Baja California (Miller and Lea 1972; Eschmeyer et al. 1983). Adults are usually collected at depths from 18 to 90 m (based on Natural History Museum of Los Angeles County (LACM) and California Academy of Sciences (CAS) adult collection data); occasionally they range beyond these limits, being found in the intertidal zone and as deep as 201 m (Love and Lee 1974). The period of peak occurrence of prespawning females for *I. quadriseriatus* ranges from January to April, but mature oocytes have been found in females in every month except October (in one year of a 2-yr study) indicating an almost year-round spawning capability (Goldberg 1980).

MATERIALS AND METHODS

Adult *I. quadriseriatus* were collected by otter trawl off Santa Monica, CA, on 8 February 1981, 3 July 1981, and 11 March 1982 and off of Huntington Beach, CA, on 19 March 1981. The females were separated from the males (easily recognized by their darkly pigmented anal fin and gill membranes) and their eggs stripped into petri dishes filled with seawater. Sperm stripped from the males was then added to selected clutches of eggs while other clutches were left unfertilized. One clutch from the spawn of July 1981 and two clutches from the spawn of March 1981 were split in half and only one-half was fertilized.

The eggs were incubated in natural seawater in a refrigerated 227 L tank with undergravel filter and within a temperature range of 13°-16°C (the March 1981 spawn was kept at 14°-16°C). The egg clutches were kept separate in plastic containers each with its own airstone. For the last spawning, March 1982, the undergravel filter was not used and the gravel removed completely in an attempt to cut

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down on bacterial and nematode infestation. The seawater was initially UV sterilized and filtered before use in the tank. Ten percent of the water was replaced every week.

The developing eggs of the first three spawnings were sampled every 2 hours for the first 12 hours and then only once a day. The eggs of the last spawning, March 1982, were sampled at 16, 38, 63, 89, and 110 hours and 6, 8, and 10 days. Living eggs were illustrated using a Wild M5[3] dissecting microscope with camera lucida. Measurements of egg diameter, perivitelline space, and oil globule diameter were taken with an ocular micrometer.

After hatching the larvae were put into 10 L plastic buckets and later transferred to the main culture tank. Ten percent of the water was changed every day. The larvae were fed the rotifer, *Brachionus plicatilis* (Hunter 1976; Misitano 1978). For the March 1982 spawn the culture tank bloomed initially with algae, including species of *Tetraselmas* and *Isochrysus*. Fresh rotifers and algae were added daily. After 20 days, *Artemia salina* nauplii were added in addition to the rotifers.

The reared larvae were sampled and viewed at hatching and every day thereafter for 12 days, and then less frequently thereafter up to 35 days. A total of 40 larvae were preserved in 4% formalin after being tranquilized with dilute quinaldine. Twenty-five larvae were preserved for analysis of pigment characteristics and morphometric comparison. Length was recorded as notochordal (NL), flexion (FL), or standard (SL) depending on the stage of caudal fin development. Selected sizes of preserved specimens were drawn using the camera lucida.

Field-collected larvae were obtained from the King Harbor Ichthyoplankton collection and the Bightwide Ichthyoplankton Program collection (LACM). Two juveniles (LACM 21639, 43579-1) were obtained from the LACM adult fish collection. Additional specimens were obtained from Marine Ecological Consultants (MEC) of Encinitas, CA. The larva from the King Harbor Ichthyoplankton collection was collected in King Harbor using a single conical 1 m diameter plankton net with 335 μm mesh towed just below the surface (McGowen 1978). A total of 420 larvae was collected by the Bightwide Ichthyoplankton Program along the California coast between Point Conception and the Mexican border using either an Auriga net (benthic sampler) or a 70 cm diameter bongo net for oblique and middepth tows (R. J. Lavenberg pers. commun.[4] and G. E. McGowen pers. commun.[5]). A 16.3 mm juvenile was collected by the Bightwide Ichthyoplankton Program with an Auriga net set with 2 mm diameter mesh. Five specimens from MEC were collected off San Onofre, CA, and the Santa Margarita River, CA, using an Auriga net (W. Watson pers. commun.[6]). Transforming larvae >10.5 mm and <16.3 mm were absent from the above collections.

Sixteen specimens were double-stained for bone and cartilage using alizarin red and alcian blue stains (Dingerkus and Uhler 1977) including one juvenile (LACM 43579-1). Eleven specimens including the juvenile were used for meristic counts.

Field-collected larvae were identified by comparing the pigmentation and myomere counts of smaller size larvae (2.7-5.8 mm) with reared larvae and by comparing larger size larvae (<9.3 mm) with cleared and stained specimens identified using vertebral, dorsal fin, anal fin, and pelvic-fin ray counts. A 10.5 mm larva was identified by meristics, including radiograph vertebral counts, and consistent spine and pigment development. A total of 425 field-collected larvae was examined; 55 larvae and 2 juveniles were observed for detailed pigment characteristics, morphometrics, and meristic counts.

Definition of terms

Preanal length = distance from the snout to a vertical line through the anus.

Body depth = depth of body at the pectoral fin base.

Pectoral fin length = horizontal distance from upper fin base to posterior edge of fin or end of longest ray.

Head length = distance from snout to posterior edge of opercle.

Flexion length (FL) = distance from the snout to the posterior tip of notochord during the stage when the posterior notochord starts to bend upward until the stage when the hypural plates are formed and in their permanent orientation, their posterior edges almost vertical.

Eye diameter = horizontal diameter of eye.

Pectoral insertion = ventral attachment of pectoral fin.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]R. J. Lavenberg, Natural History Museum of Los Angeles County Section of Fishes, 900 Exposition Boulevard, Los Angeles, CA 90007, pers. commun. winter 1982.

[5]G. E. McGowen, Natural History Museum of Los Angeles County, Section of Fishes, 900 Exposition Boulevard, Los Angeles, CA 90007, pers. commun. winter 1982.

[6]William Watson, Marine Ecological Consultants, 531 Encinitas Boulevard, Suite 110, Encinitas, CA 90024, pers. commun. summer 1981.

Trunk = muscular section of body not including the head, abdominal cavity or caudal fin.

RESULTS

Fertilization

Eight whole egg clutches were externally fertilized with freshly stripped sperm, and five contained eggs that developed successfully into the embryo stage. Three whole egg clutches were left unfertilized, and none contained eggs that developed successfully into the embryo stage. Three whole egg clutches were split in half; one half was fertilized with sperm and the other was left unfertilized. Eggs in all three of the fertilized halves developed successfully into the embryo stage; eggs in the unfertilized halves did not. Therefore, there was no evidence of internal fertilization.

Egg Description

Icelinus quadriseriatus eggs are adhesive and negatively buoyant after being stripped from the female and formed a single clutch of 200-250 eggs (excluding eggs that may have been left in the abdomen; Goldberg [1980] reported an average clutch size of 284 eggs in 28 gravid fish). The eggs are 1.08-1.17 mm in diameter and are initially transparent, but the chorion becomes more opaque and textured during development. A pale-green yolk fills most of the egg except for a small perivitelline space (0.024-0.096 mm).

At spawning there are about 15 yellow oil globules, the largest of which is 0.14 mm in diameter, which coalesce to one oil globule of 0.14-0.19 mm diameter by the eighth day of development. An opaque, flocculant mass is suspended in the yolk next to the oil globules.

Embryonic Development

The eggs develop for 12-13 days in 13°-16°C seawater before hatching. Sixteen hours after artificial fertilization the blastodisc is well formed (Fig. 1A). By 38 h the eggs are in the crescent stage of gastrulation (Fig. 1B). The germ ring can be seen making its way around the yolk. At 63 hours somites begin to form along the embryo and the eye capsule is present (Fig. 1C). At 89 hours the heart (Fig. 1D), brain, and otic capsules are visible, and the body is lined with 30 or more myomeres. The heart begins beating after 110 hours, and the vitelline veins can be seen coursing across the surface of the yolk (Fig. 1E). At 6-7 days the anus forms, the eyes become darkly pigmented (Fig. 1F), and the tail begins flexing back and forth. A patch of tubercles forms on the interorbital section of the head and persists until immediately after hatching.

At 7-8 days the embryos develop pectoral buds (Fig. 1G) and melanophores begin forming on the anus and surrounding yolk sac. The eyes turn a metallic green and blood begins circulating through the ventral veins and arteries of the body.

Numerous melanophores cover the yolk sac, anus, and postanal ventral midline (Fig. 1H) in late-stage embryos. The head flattens against the chorion and the tubercles spread from the snout to just dorsal to the otic capsule.

After 10-12 days eggs reared at 13°-16°C begin to hatch.

Description of Larvae

The larvae hatch with the oil globules positioned at the anterior of the yolk sac (Fig. 2A). The yolk is absorbed after 6-7 days. The oil globules disappear along with the yolk in reared larvae; whereas, the oil globule(s) in field-collected larvae move about the abdominal cavity, are fragmented, possibly increase in diameter, or are absent completely (Fig. 2B-C). Evidence of the globule's increase in diameter in the field-collected larvae is found in some specimens (6.1-8.0 mm SL) with oil globules from 0.26 to 0.36 mm diameter, about twice the diameters of oil globules in the eggs and yolk-sac larvae.

The percentage of field larvae with oil globules (based on a subsample of 129 larvae) drops from 93% in larvae with yolk sacs (N = 15) to 70% in larvae <3.5 mm (N = 79) to 45% in larvae 3.6-6.0 mm (N = 20) to 27% in larvae 6.1-8.0 mm (N = 15). Larvae over 8.0 mm possess minute or no oil globules.

Reared larvae hatch at 2.7-3.4 mm NL (after preservation); field-collected larvae are found as small as 2.6 mm. The larvae shorten to a varying degree, depending probably on the reaction to quinaldine and Formalin. Reared larvae shrink 5-17% after anesthesia and fixation.

Myomere counts range from 31-37. Double-stained specimens have vertebral counts of 33-35.

Morphometrics are given in Table 1. From 6.0 to 9.4 mm the larvae become more deep-bodied (27-30% SL) and the head length increases to 34% of the standard length.

A pigmented preanal finfold does not preserve in the field larvae as it does in the laboratory-reared larvae. There is a skin connection between the anus and the rest of the gut, usually with one or more

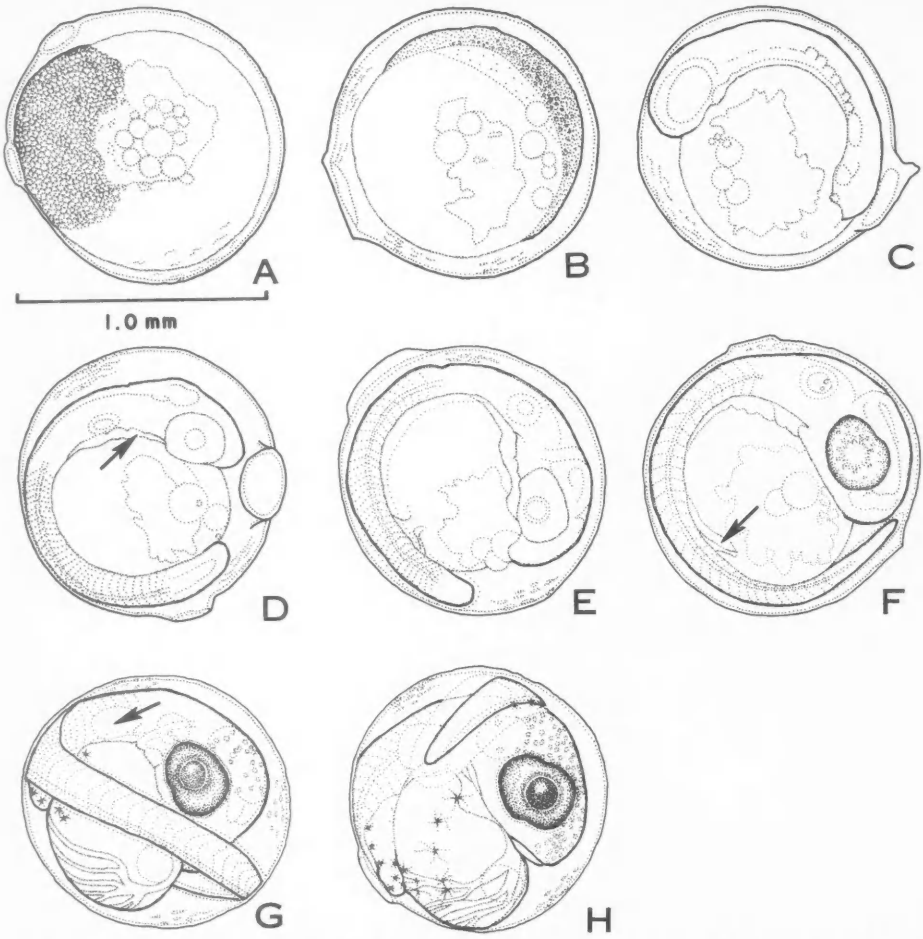

FIGURE 1—Eggs of *Icelinus quadriseriatus*: A) 16 hours (LACM 44159-1); B) 38 hours (LACM 44159-2); C) 63 hours (LACM 44159-3); D) 89 hours (LACM 44159-4), arrow indicates heart; E) 110 hours (LACM 44159-5); F) 6 days (LACM 44159-6), arrow indicates anus; G) 8 days (LACM 44159-7), arrow indicates pectoral bud; H) 10 days (LACM 44159-8).

melanophores, but it is not formed into a finfold as in the reared larvae.

Pigmentation

Pigment in the larvae at hatching is restricted to the postanal ventral midline, the ventral abdominal surface, the dorsoposterior peritoneum, the anus, and the lower jaw angle (Fig. 2A). The postanal ventral midline melanophores are positioned in a single row, number from 25 to 37 in yolk-sac larvae and increase to a maximum of 63 in larvae 3.5-4.0 mm in length. These melanophores decrease to a minimum of 25 in larvae 5.5 mm or larger. The ventral

FIGURE 2.—Field-collected and reared *Icelinus quadriseriatus* larvae: A) 2.8 mm (LACM 025-RB-36-AU-01); B) 3 days old (reared), 3.9 mm (LACM 44160-1); C) 4.6 mm (LACM 012-88-36-BB-01); D) 6.6 mm (LACM 012-88-36-BB-01); E) Ventral view, 6.6 mm.

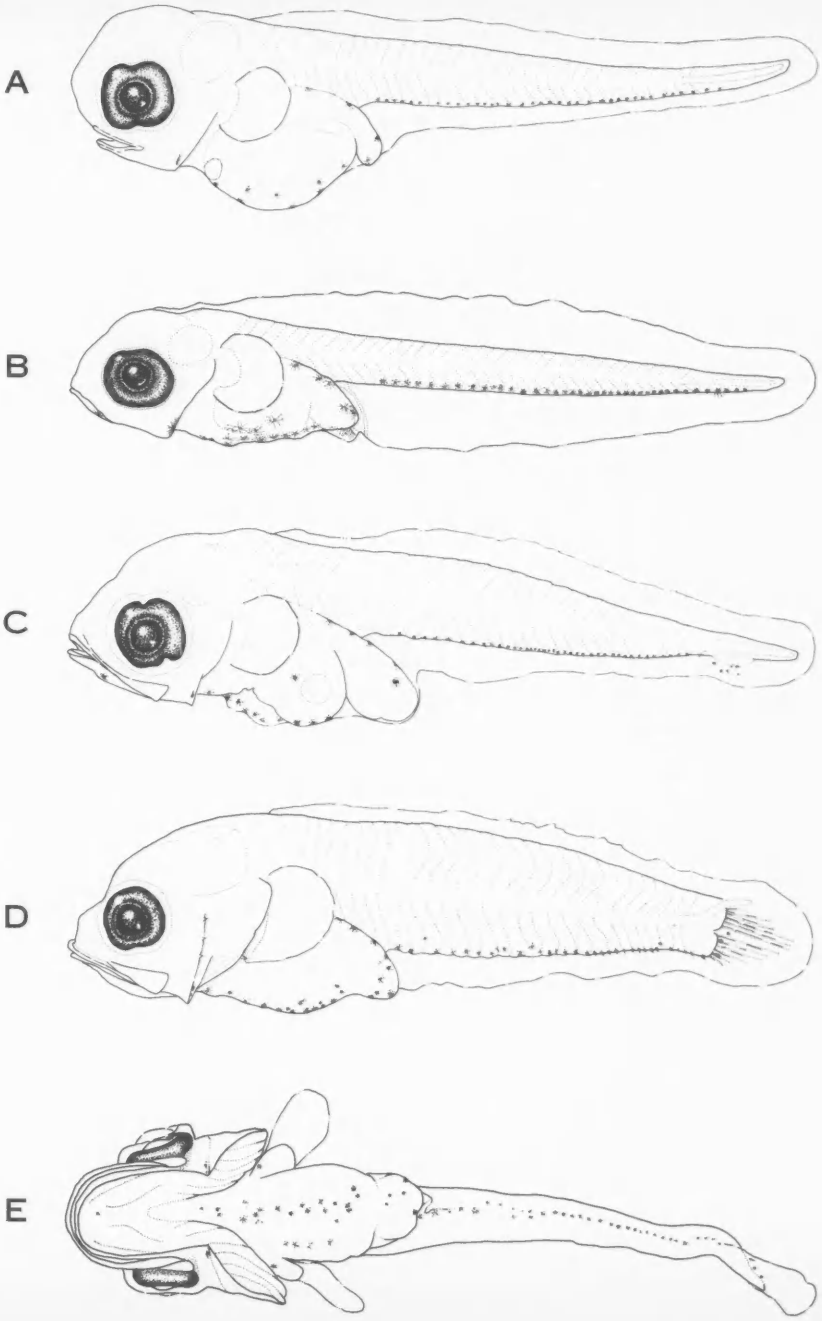
A
B
C
D
E

TABLE 1.—Morphometrics of *Icelinus quadriseriatus* larvae, represented as a mean percentage ($\bar{x}_p$) of body length, with a range (r) of percentages and a standard deviation (SD). Specimens between dashed lines are undergoing flexion of the notochord. * = reared larvae.

Size range (mm)	N	Preanal length			Body depth			Pectoral fin length			Head length			Eye diameter		
		$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD
2.5-2.9	4	42.0	(38.5-46.1)	4.1	29.6	(25.2-31.9)	3.0	5.9	(5.2-6.8)	0.9	24.0	(20.4-26.2)	2.5	11.3	(9.6-12.2)	1.2
*2.5-2.9	4	47.5	(41.1-51.7)	4.7	25.3	(23.5-27.5)	1.7	8.4	(4.3-13.1)	3.9	25.3	(22.1-28.5)	2.6	12.2	(11.1-14.1)	1.3
3.0-3.4	4	41.2	(39.1-45.0)	2.7	23.8	(21.8-25.5)	2.0	9.1	(7.9-11.0)	1.5	23.0	(21.8-24.7)	1.3	10.9	(10.3-11.3)	0.4
*3.0-3.4	7	45.9	(41.2-51.3)	3.8	21.7	(19.1-24.2)	2.1	9.4	(7.1-12.1)	1.7	23.6	(18.2-26.7)	2.8	11.3	(10.0-12.4)	0.9
3.5-3.9	4	43.0	(41.0-44.0)	1.4	22.9	(21.1-26.6)	2.5	7.4	(6.6-8.7)	0.9	22.8	(21.1-25.1)	1.7	10.2	(9.7-10.9)	0.5
*3.5-3.9	8	39.5	(34.4-50.5)	4.9	19.0	(15.8-28.5)	4.2	10.7	(7.4-16.7)	2.7	21.3	(17.6-31.5)	4.6	9.7	(8.2-13.6)	1.8
4.0-4.4	4	43.0	(40.0-47.5)	3.3	24.9	(21.0-28.2)	3.0	9.3	(7.3-10.3)	1.4	24.5	(23.0-26.1)	1.3	9.9	(9.0-10.8)	0.7
*4.0-4.4	3	39.7	(36.8-43.2)	3.2	20.4	(15.2-25.2)	5.0	10.5	(6.6-14.8)	4.1	23.1	(19.1-26.6)	3.8	9.9	(8.2-11.1)	1.5
4.5-4.9	4	46.0	(41.9-47.8)	3.2	23.8	(22.1-27.3)	2.4	7.4	(6.8-8.0)	0.6	22.4	(19.4-25.9)	2.8	9.3	(8.9-10.0)	0.9
*4.5-4.9	2	45.0	(40.9-49.1)	5.8	24.6	(23.1-26.0)	2.1	12.5	(10.7-14.2)	2.5	27.5	(27.3-27.6)	0.2	11.7	(11.6-11.8)	0.1
5.0-5.4	4	45.6	(44.0-48.7)	2.1	24.9	(21.1-27.7)	2.8	7.4	(5.5-9.2)	1.6	23.4	(20.4-26.2)	2.6	9.1	(8.5-10.0)	0.7
5.5-5.9	4	44.9	(43.6-48.0)	2.1	26.5	(25.3-28.0)	1.2	8.7	(6.5-10.5)	1.7	25.4	(22.5-27.5)	2.3	9.3	(8.7-10.0)	0.6
*5.5-5.9	1	48.6			26.6			14.8			29.7			11.0		
6.0-6.4	4	49.2	(46.1-54.7)	3.7	27.3	(25.9-28.3)	1.4	9.1	(7.5-11.4)	1.8	27.5	(24.4-30.2)	2.4	8.7	(8.3-9.2)	0.4
6.5-6.9	4	46.0	(44.3-49.9)	2.7	27.2	(24.4-31.2)	3.0	11.5	(8.1-15.7)	4.6	29.4	(25.3-33.9)	3.9	8.9	(8.4-9.4)	0.4
7.0-7.4	4	46.7	(44.1-52.2)	3.2	27.8	(25.4-29.1)	1.5	12.1	(9.3-14.9)	2.9	27.9	(24.7-31.5)	2.5	8.8	(8.5-9.2)	0.3
7.5-7.9	3	48.7	(47.0-49.7)	1.5	27.5	(27.2-27.9)	0.4	17.2	(16.3-18.3)	1.0	30.2	(29.5-31.2)	0.9	9.3	(8.7-9.6)	0.5
8.0-8.4	2	50.7	(47.7-53.6)	4.2	29.0	(27.3-30.7)	2.4	19.7	(15.9-23.5)	5.4	29.8	(29.6-30.0)	0.3	9.6	(8.9-10.2)	0.9
8.5-8.9	4	51.5	(49.4-53.2)	1.6	30.8	(27.4-33.9)	2.7	22.3	(21.1-24.2)	1.3	34.4	(32.4-37.3)	2.4	9.5	(8.7-9.9)	0.5
9.0-9.4	4	52.2	(50.9-54.0)	1.3	29.7	(29.3-30.0)	0.3	23.9	(22.5-25.1)	1.2	33.8	(31.1-36.7)	2.3	9.3	(8.7-10.2)	0.7
9.5-10.4	—	—			—			—			—			—		
10.5	1	51.4			25.6			32.2			39.1			11.1		
16.3	1	51.5			22.7			28.8			36.8			11.0		
18.7	1	46.5			26.7			24.6			37.9			9.1		

abdominal pigment consists of 1-6 rows of melanophores aligned anteroposteriorly (Fig. 2E). The dorsal peritoneal pigment consists of 2-5 melanophores in a double row over the posterior half of the gut, increasing to a maximum of 17 in a 5.8 mm reared larva. There are usually 3-5 melanophores surrounding the anus in newly hatched larvae and up to 12 in the larger larvae. There is always a distinct melanophore on the lower jaw angle.

As the larvae grow they develop melanophores on the isthmus (throat), chin, pectoral insertion, anterior gut (usually 2 melanophores slightly internal from the ventral abdomen), head, and dorsal body (Table 2). Reared larvae >4.0 mm possess considerably more pigment (based on the number of melanophores) on the dorsal body and the anterior gut areas than field larvae of the same size.

The larvae undergo flexion between 5.2 mm and 7.6 mm (reared larvae 4.5-5.8+ mm). Melanophores (1-4) are usually present on the caudal fin anlage and later at the base of the caudal fin. In flexion and postflexion larvae the caudal fin base melanophores are present in over 95% of the specimens.

Postflexion larvae (8.0-9.3 mm SL) develop numerous small punctate melanophores over the midbrain portion of the cranium (Fig. 3A). Melanophores form between the otic capsule and the hindbrain. Melanophores occur on the preopercle between the eye and the fourth preopercular spine. There are 1-3 melanophores at the pectoral insertion, 3-6 melanophores along the pectoral base, and a circle of 7-9 small melanophores dorsal to the pectoral origin. There are 4-11 small melanophores ventral to the eye and dorsal to the maxillary bone and 1 melanophore at the posteroventral edge of the maxillary. Several melanophores occur along the edge of the mandible from the articular to the dentary bone. Four to five minute melanophores are situated between the eye and premaxillary bone. The ventral abdomen becomes sprinkled with 40-45 melanophores.

Transition from larval to juvenile pigmentation starts at about 9.2-9.5 mm SL. Transforming larvae develop four patches of melanophores on the dorsal trunk and three patches on the lateral trunk (Fig. 3B). Melanophores appear on the dorsal and caudal fins. In larger specimens (Fig. 3C) the head and dorsolateral pigment takes on the juvenile pattern. The dorsal and lateral trunk melanophores merge forming three dorsolateral bars on the body. Distinct patches of melanophores cover the hypural

FIGURE 3.—Field-collected *Icelinus quadriseriatus* postlarvae and juvenile (D): A) 9.3 mm (LACM 012-88-36-BB-01); B) 9.2 mm (MEC I48 Stn. E Rep. #2); C) 10.5 mm (MEC I-89, E-LS EPI); D) 18.7 mm (LACM 21639).

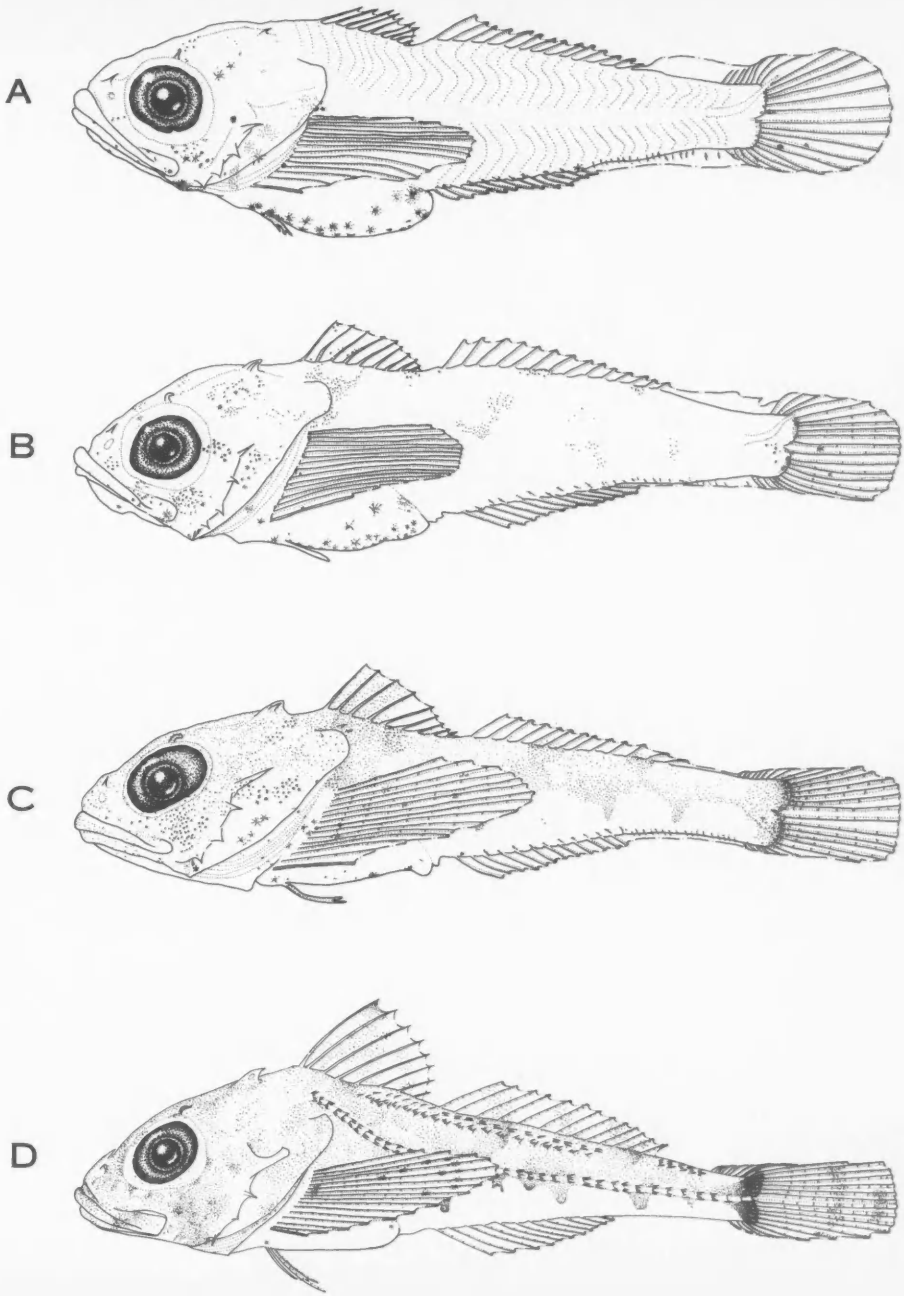
A
B
C
D

TABLE 2.—Presence of melanophores at described locations in *Icelinus quadriseriatus* larvae, represented as a percentage of larvae showing the melanophoes. * = reared larvae.

Size range (mm)	N	Lower jaw angle	Isthmus (throat)	Chin	Pectoral insertion	Anterior gut	Head (dorsal)	Dorsal trunk
2.5-2.9	4	100.0	0.0	0.0	0.0	25.0	0.0	0.0
*2.5-2.9	4	100.0	25.0	0.0	0.0	0.0	0.0	0.0
3.0-3.4	4	100.0	0.0	0.0	0.0	0.0	0.0	0.0
*3.0-3.4	7	100.0	14.3	42.9	14.3	0.0	14.3	14.3
3.5-3.9	4	100.0	75.0	50.0	25.0	0.0	0.0	0.0
*3.5-3.9	8	100.0	75.0	62.5	50.0	12.5	37.5	25.0
4.0-4.4	4	75.0	25.0	50.0	0.0	0.0	0.0	0.0
*4.0-4.4	3	100.0	100.0	100.0	100.0	66.7	33.3	0.0
4.5-4.9	4	100.0	25.0	50.0	0.0	0.0	0.0	0.0
*4.5-4.9	2	100.0	100.0	100.0	100.0	50.0	50.0	50.0
5.0-5.4	4	100.0	50.0	25.0	25.0	0.0	0.0	0.0
5.5-5.9	4	100.0	100.0	0.0	25.0	25.0	0.0	0.0
*5.5-5.9	1	100.0	100.0	100.0	100.0	100.0	100.0	100.0
6.0-6.4	4	100.0	100.0	25.0	50.0	25.0	0.0	0.0
6.5-6.9	4	100.0	100.0	25.0	50.0	0.0	0.0	0.0
7.0-7.4	5	100.0	80.0	40.0	0.0	20.0	0.0	20.0
7.5-7.9	3	100.0	100.0	0.0	66.7	0.0	0.0	0.0
8.0-8.4	2	100.0	100.0	0.0	100.0	0.0	0.0	0.0
8.5-8.9	3	100.0	100.0	66.7	100.0	33.3	33.3	33.3
9.0-9.4	5	100.0	100.0	80.0	100.0	60.0	80.0	20.0

plates. The ventral abdomen and postanal ventral melanophores begin to fade and become less numerous.

Transformed juveniles (including a 16.3 mm specimen, LACM 056-OB-75-JA01) display most adult characters (Bolin 1944) including a double row of scales just ventral to the dorsal fin (Fig. 3D). A gap in the scale row is located below the insertion of the second dorsal fin. Melanophores almost disappear from the postanal and ventral midline and concentrate on the head, dorsal body, and fins. There is a concentration of pigment between the eye and the lower jaw angle and at the base of the caudal fin.

Meristic Elements

Ray elements of the pectoral and caudal fins start developing in larvae 6.8-7.0 mm long. Spine and ray elements of the dorsal and anal fins develop at about 7.4-7.6 mm. The pelvic fin elements are countable in specimens that are double stained and at least 8.2 mm SL (Table 3).

The fin and vertebral counts of 10 double stained field-collected larvae 7.4-8.9 mm long and one juvenile 27.8 mm SL correspond closely to the counts of 36 x-rayed adults from the LACM collection. These counts are consistent with x-ray count frequencies given in Howe and Richardson (1978) except for the dorsal spine counts. The most frequent dorsal spine count listed in Howe and Richardson was eight whereas in the LACM specimens it was nine. It is possible that there is some slight variability in this meristic character or the last (inconspicuous) dorsal spine may have been overlooked in the former's x-ray counts.

TABLE 3.—Meristics of *Icelinus quadriseriatus* larvae. ND = no data (specimens between the dashed lines are undergoing flexion of the notochord). * = reared larvae; + = cleared and stained larvae; ° = x-rayed.

Size (mm SL)	Dorsal fin spines	Dorsal fin rays	Anal fin rays	Pectoral fin rays (left)	Pectoral fin rays (right)	Pelvic fin spines and rays (left)	Pelvic fin spines and rays (right)	Preopercle spines	Precaudal vertebrae	Caudal vertebrae	Total Vertebrae	Myomeres	Postanal ventral melanophores
*2.7	—	—	—	—	—	—	—	—	—	—	—	34	33
3.5	—	—	—	—	—	—	—	—	—	—	—	34	42
4.7	—	—	—	—	—	—	—	—	—	—	—	34	32
+5.3	—	—	—	—	—	—	—	—	—	—	—	34	44
5.7	—	—	—	—	—	—	—	—	—	—	—	36	38
*5.8	—	—	—	—	—	—	—	—	—	—	—	34	34
6.6	—	—	—	—	—	—	—	—	—	—	—	34	34
+6.8	—	—	—	11	11	buds	buds	2	ND	ND	ND	35	26
+7.4	IX	12	11	16	16	—	—	4	10	24	34	ND	30
+7.6	—	—	12	12	14	buds	buds	3	ND	ND	ND	35	27
7.7	IX	14	13	15	16	buds	buds	4	ND	ND	ND	33	28
+8.2	X	15	13	16	16	I,2	I,2	4	11	22	33	ND	34
+8.5	VIII	14	12	16	16	I,2	I,2	4	11	23	34	ND	31
°9.2	IX	14	12	16	16	I,2	I,2	4	ND	ND	34	35	29
°9.3	IX	14	12	16	16	I,2	I,2	4	ND	ND	34	34	32
°10.5	IX	13	12	15	16	I,2	I,2	4	ND	ND	33	33	28
°16.3	IX	14	12	16	16	I,2	I,2	4	11	23	34	ND	8
°18.7	VIII	13	11	16	16	I,2	I,2	4	10	24	34	ND	4

Ossification

Ossification begins in larvae at least 5.3 mm NL long. The cleithrum, premaxilla, maxilla, mandible, parts of the neurocranium, and 3 of 6 branchiostegal rays on each side are ossified. The first 14 vertebrae, the middle 10 out of 12 principal caudal rays, 11-13 pectoral rays, 2-3 preopercular spines, and opercle bone, and all of the branchiostegal rays become ossified at 6.8-7.0 mm.

Ossification is well developed in specimens 7.4 mm FL long or greater. The nasal, quadrate, dorsal spines, and the first 28 of 33 vertebrae become ossified as well as the hypural plates and all of the principal caudal rays.

A double row of teeth appears on the lower jaw of double-stained larvae between 6.8 and 7.4 mm FL in length. On the upper jaw a single row of teeth is seen in larvae 8.5 mm SL or greater in length.

Spination

One to three preopercular spines appear at 6.5-7.0 mm FL. Four preopercular spines are visible in larvae over 7.0 mm FL. Nasal and parietal spines form at 9.0-9.3 mm SL. Double-stained material shows the parietal spine arising from two arcs of bone that fuse distally into one spine before breaking the surface of the skin. A foramen remains in the center of the spine and is retained in the parietal spines of juveniles and adults.

Development of the Caudal Complex

The caudal fin anlage begins to form in preflexion larvae of about 5.3 mm NL (Fig. 4A). During flexion three non-ossified hypural elements form ventral to the notochord (Fig. 4B). The first hypural (identified as HY_{1-3}) may be a remnant of a fusion process of two to three elements. Matarese and Marliave (1982) described three elements that fuse to form the inferior hypural plate in *Ascelichthys rhodorus*; a foramen is left where the parhypural (counted as HY_1) fuses with HY_2 and HY_3. In *I. quadriseriatus* a foramen is present in HY_{1-3}.

The second and third hypural elements (HY_4 and HY_5) form separately (Fig. 4B-C) and fuse to form the ossified superior hypural plate (HY_{4-5}) (Fig. 4D). Finally, the two plates (HY_{1-3} and HY_{4-5}) begin to fuse anteriorly in juveniles (Fig. 4D).

Cartilaginous neural spines begin to form during flexion (Fig. 4B). By about 8.7 mm SL the neural spine on the first preural centrum (PU_1) appears (on one specimen) as two distinct elements (Fig. 4C).

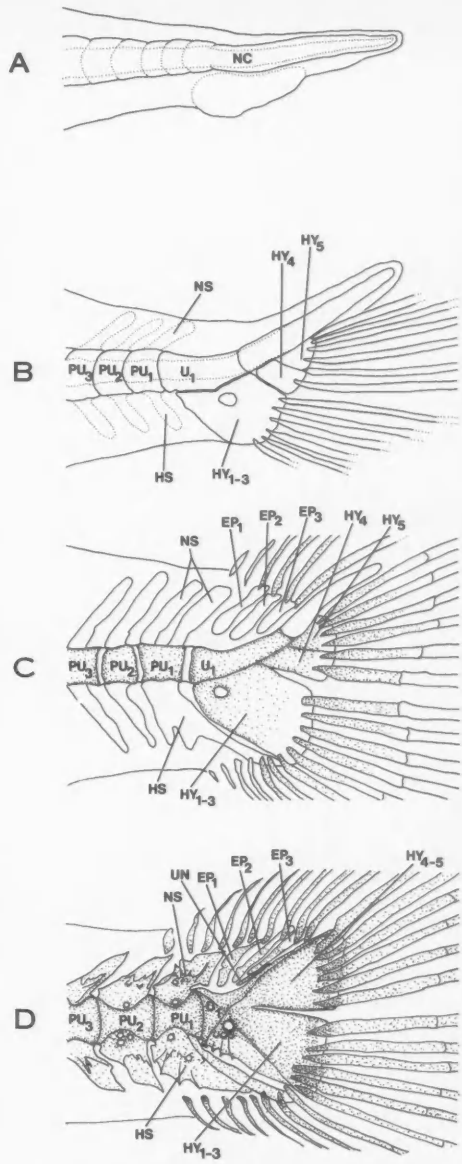

FIGURE 4.—Caudal complex of *Icelinus quadriseriatus*: A) 5.3 mm (LACM 012-88-36-BB-01); B) 6.8 mm (LACM 012-88-36-BB-01); C) 8.7 mm (LACM 012-88-36-BB-01); D) 27.8 mm (LACM 43579-1). EP = epural; HS = hemal spine; HY = hypural; NC = notochord; NS = neural spine; PU = preural centra; U = urostyle; UN = uroneural.

This condition has been illustrated in one other larval sculpin (Matarese and Marliave 1982, Fig. 2E), but may be variable. By the juvenile stage the neural element(s) appear as one broad, ossified spine (Fig. 4D).

Hemal spines form in unison with the neural spines. The hemal spine on the first pre-ural centrum develop an elongate, descending process to which several procurrent rays articulate. A similar elongate structure was identified as the parhypural in *Icelus spiniger* (Nelson 1984). The present study agrees with Materese and Marliave (1982) and Yabe (1985) in identifying the process as part of the hemal spine because it is always associated with the spine during development.

Twelve principal caudal rays develop and articulate with the hypural plates during flexion (Fig. 4B). The number of these rays varies in other sculpins from 11 to 13 (Materese and Marliave 1982; Nelson 1984).

Procurrent rays form after flexion (Fig. 4C) and increase in number to a maximum of 10 for the upper procurrent rays and 8 for the lower procurrent rays. The last lower procurrent ray appears to articulate with a radial cartilage between the posterior tip of the descending hemal spine process and the anteroventral edge of the inferior hypural plate.

Three epurals form dorsal to the ural-centrum in the postflexion larvae and are also present in juveniles and adults. A uroneural appears dorsal to the reduced urostyle in the juveniles (Fig. 4D).

Occurrence

Icelinus quadriseriatus larvae were collected in every month of the year with peak occurrence from May to June in 1979, which is in agreement with peak occurrence of prespawning females (Goldberg 1980) for 1977, allowing for a time lag between prespawning condition and hatching of the larvae; the larvae are assumed to be planktonic for about 2 months. Peak spawning periods may vary yearly. Goldberg (1980) reported a winter peak of oocyte development that was earlier in 1978 (January-April) than in 1977 (March-June).

In the Southern California Bight, *I. quadriseriatus* larvae seemed to be concentrated in deeper waters away from the intertidal and shallow subtidal areas. Of the 33 bightwide discrete depth samples (nueston, middepth, and epibenthic) collected in 1979 in which *I. quadriseriatus* occurred, only 2 samples were taken at the 8 or 15 m depth stations. Ten samples were taken at the 22 m stations and 21 samples were taken at the 36 m station.

Icelinus quadriseriatus larvae were generally found near the bottom of the water column. Of the 33 discrete depth tows taken in which *I. quadriseriatus* larvae were found, 31 were epibenthic tows and two were middepth tows.

The bottom temperature at stations where *I. quadriseriatus* larvae occurred ranged from 11° to 14°C. Since the larvae were usually found at the bottom, this suggests that these are the temperatures under which they normally develop in the field. Reared larvae were observed to survive aquarium temperatures of at least 18°C.

DISCUSSION

Fertilization

Many cottids, including *Chitonotus* and *Oligocottus snyderi*, practice internal fertilization facilitated by an intromittent male sex organ (Morris 1956; Hubbs 1966; Stein 1973; Misitano 1980). Bolin (1941) reported that *Orthonopias triacis* has internal fertilization even though the males do not have an external penis. Apparently the female has a "protrusile oviduct" which is probably smeared with sperm and then retracted. Fertile eggs have been removed from females of *Scorpaenichthys marmoratus* and *Icelinus filamentosus* (Hubbs 1966). *Icelinus quadriseriatus* males possess no external penis and since no females were found with fertile eggs, it is still questionable as to what mode of fertilization these sculpins possess. It is possible that *I. quadriseriatus* has external fertilization (a rarity among sculpins), but until the mating process is observed or an internally fertilized female is found, this question will remain unanswered.

Comparison with Other Sculpin Eggs

The eggs of *I. quadriseriatus* are adhesive, demersal, and share many characteristics with other cottid eggs. The presence of a flocculant mass inside the yolk has been observed in several other genera such as *Chitonotus*, *Orthonopias*, *Clinocottus*, and *Leptocottus* (Bolin 1941; Morris 1951; Jones 1962; Misitano 1980). Multiple oil globules that coalesce to one globule are common in other sculpins; however, *I. quadriseriatus* does have the highest initial number of oil globules (15) recorded in the literature. The diameters for *I. quadriseriatus* eggs are closest to the diameters of *Artedius lateralis* and *Clinocottus analis* eggs (Budd 1940).

The pale-green color of the yolk and the pigmentation of the late-stage embryo are most similar to

Chitonotus pugetensis eggs (Goldberg 1980; Misitano 1980). (The eggs of other *Icelinus* species have not been described and could not be used for comparison.)

The appearance of tubercles on the head of the late-stage embryos has been observed in several other cottid species. Budd (1940) described them in *Artedius lateralis* and *Clinocottus analis* as a "patch of minute nodules" which are "believed to aid as a rasp in breaking through the shell... allowing the larva to escape anterior end foremost". Bolin (1941) referred to them in *Orthonopias* as a "large number of small granular patches". Morris (1951) described them in *Clinocottus recalvus* as "minute convexities of low elevation which grade into the dorso-anterior surface of the head" and are formed due to the "the extreme pressure which it suffers during its late stages of confinement". In the case of *I. quadriseriatus* the head does flatten in the late-stage embryos and may be under pressure, but whether these structures form in response to that pressure is not known. The tubercles may serve only to reinforce the area of the head which pushes its way through the chorion.

Distinguishing Larval Characters

Distinguishing characters include 1-6 rows of ventral gut melanophores, 25-63 postanal ventral melanophores, and a distinct lower jaw angle melanophore on either side. An increasing percentage (25-100%) of larvae over 3.5 mm in each size class develop isthmus, chin, and pectoral insertion melanophores.

Icelinus quadriseriatus larvae are characteristic of the *Paricelinus/Triglops/Icelus/Chitonotus/Icelinus* group of Richardson (1981) which is distinguished by four preopercular spines, a pointed snout, moderately slender body, and postanal pigment restricted to ventral midline.

Paricelinus, *Triglops*, and *Icelus* all have a higher number of vertebrae: 40-42, 44-54, and 37-44 respectively (Washington et al. 1984), than *I. quadriseriatus*. *Paricelinus hopliticus* in addition has pigment on the snout, nape, and anterior gut in preflexion larvae.

Chitonotus pugetensis larvae, while similar in appearance to yellowchin larvae, differ in having several anterior gut melanophores, an early development of head pigment and a slightly higher range of vertebrae (35-36). Larger (6.0-9.4 mm) *C. pugetensis* are more slender-bodied (23-25% SL) (Richardson and Washington 1980) than *I. quadriseriatus* SL (27-30%). In transforming *C. pugetensis* larvae there are usually three pelvic fin rays and a nuchal spine next to the parietal spine while *I. quadriseriatus* has only two pelvic rays and no nuchal spine. The fin ray counts of *C. pugetensis* (Howe and Richardson 1978) are somewhat higher than the yellowchin, especially the anal fin rays (14-17, $\bar{x}$ = 15.7, in *C. pugetensis*; 10-13, $\bar{x}$ = 12.1, in *I. quadriseriatus* larvae).

Artedius creaseri and *A. meanyi*, recently added to this group (Washington 1986), have anterior gut pigment, pigment in the ventral finfold and fewer postanal ventral melanophores (<13). Postflexion *A. creaseri* and *A. meanyi* larvae have nuchal spines next to the parietal spines.

Seven species of *Icelinus*, all with undescribed larval stages, co-occur with *I. quadriseriatus* in the Southern California Bight, including one undescribed species (R. Rosenblatt fn. 2). Several larvae have recently been collected at a 75 m depth station (LACM) that are very similar to field-collected *I. quadriseriatus* larvae including possession of lower jaw angle, chin, isthmus, and pectoral insertion melanophores. A cleared and stained specimen has a count of 38 vertebrae that identifies it tentatively as *I. tenuis*. These larvae differ from *I. quadriseriatus* in having a higher myomere count (37-40), anterior peritoneal pigment similar to *Chitonotus*, and an absence of caudal melanophores.

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LITERATURE CITED

BOLIN, R. L.
1941. Embryonic and early larval stages of the cottid fish

Orthonopias triacis Starks and Mann. Stanford Ichthyol. Bull. 2:73-82.

1944. A review of the marine cottid fishes of California. Stanford Ichthyol. Bull. 3:1-135.

BUDD, P. L.

1940. Development of the eggs and early larvae of six California fishes. Calif. Div. Fish Game, Fish Bull. 56, 50 p.

DINGERKUS, G., AND L. D. UHLER.

1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52:229-232.

ESCHMEYER, W. N., E. HERALD, AND H. HAMMANN.

1983. A field guild to Pacific Coast fishes of North America. Peterson Field Guide Series 28. Houghton Miffin Co., Boston.

GOLDBERG, S. R.

1980. Seasonal spawning cycles of two marine cottid fishes, *Chitonotus pugetensis* and *Icelinus quadriceriatus* from Southern California. Bull. Mar. Sci. 30:131-135.

HOWE, K. M., AND S. L. RICHARDSON.

1978. Taxonomic review and meristic variation in marine sculpins (Osteichthyes: Cottidae) of the northeast Pacific Ocean. NOAA-NMFS Contract NO. 03-78-M02-120 rep., 142 p.

HUBBS, C.

1966. Fertilization, initiation of cleavage, and developmental temperature tolerance of the cottid fish, *Clinocottus analis*. Copeia 1966:29-42.

HUNTER, J. R.

1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

JONES, A. C.

1962. The biology of the euryhaline fish *Leptocottus armatus armatus* Girard (Cottidae). Univ. Calif. Publ. Zool. 67:321-368.

LOVE, M. S., AND R. S. LEE.

1974. New geographic and bathymetric records for fishes from Southern California. Calif. Fish. Game 60:212-216.

MARLIAVE, J. B., S. K. TODD, AND A. W. A. BAKER.

1985. Larvae of the manacled sculpin, *Synchirus gilli*, F. Cottidae. *In* A. W. Kendall Jr., and J. B. Marliave (editors), Descriptions of early life history stages of selected fishes: from the 3rd International Symposium on the Early Life History of Fishes and 8th Annual Larval Fish Conference, p. 49-54. Can. Tech. Rep. Fish. Aquat. Sci. 1359.

MATARESE, A. C., AND J. B. MARLIAVE.

1982. Larval development of laboratory-reared rosylip sculpin, *Ascelichthys rhodorus* (Cottidae). Fish. Bull., U.S. 80:345-355.

MCGOWEN, G. E.

1978. Effects of thermal effluent from Southern California Edison's Redondo Beach steam generating plant on the warm-temperate fish fauna of King Harbor Marina: Ichthyoplankton study report for phase III. South. Calif. Edison Co. project no. 2705-0456, P.O. #U0654902, series no. 78-RD-47.

MILLER, D. J., AND R. N. LEA.

1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MISITANO, D. A.

1978. Description of laboratory-reared larvae of the buffalo sculpin, *Enophrys bison* (Pisces: Cottidae). Copeia 1978: 635-642.

1980. A record of internal fertilization in the roughback sculpin *Chitonotus pugetensis* with descriptive notes of their early larvae. Copeia 1980:162-165.

MORRIS, R. W.

1951. Early development of the cottid fish, *Clinocottus recalvus* (Greeley). Calif. Fish and Game 37:281-300.

1956. Clasping mechanism of the cottid fish *Oligocottus snyderi* Greeley. Pac. Sci. 10:314-317.

NELSON, D. W.

1984. Systematics and distribution of cottid fishes of the genera *Rastrinus* and *Icelus*. Occas. Pap. Calif. Acad. Sci. 138, 58 p.

RICHARDSON, S. L.

1981. Current knowledge of larvae of sculpins (Pisces: Cottidae and allies) in northeast Pacific genera with notes on relationships within the family. Fish. Bull., U.S. 79:103-121.

RICHARDSON, S. L., AND B. B. WASHINGTON.

1980. Guide to identification of some sculpin (Cottidae) larvae from marine and brackish waters off Oregon and adjacent areas of the northeast Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ-430, 56 p.

STEIN, R.

1973. Description of laboratory-reared larvae of *Oligocottus maculosus* Girard (Pisces: Cottidae). Copeia 1973:373-377.

WASHINGTON, B. B.

1986. Systematic relationships and ontogeny of the sculpins *Artedius*, *Clinocottus*, and *Oligocottus* (Cottidae: Scorpaeniformes). Proc. Calif. Acad. Sci. 44:157-223.

WASHINGTON, B. B., W. N. ESCHMEYER, AND K. M. HOWE.

1984. Scorpaeniformes: relationships. *In* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (editors), Ontogeny and systematics of fishes, p. 438-447. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

YABE, M.

1985. Comparative osteology and myology of the superfamily Cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. Mem. Fac. Fish., Hokkaido Univ. 32:1-130.

YABE, M., K. TSUMURA, AND M. KATAYAMA.

1980. Description of a new cottid fish, *Icelinus japonicus*, from Japanese waters. Jpn. J. Ichthyol. 27:106-110.

FEEDING ECOLOGY AND GROWTH ENERGETICS OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

The relation between prey consumption and gross growth efficiency was determined for first-feeding northern anchovy, *Engraulis mordax*, fed rotifers for 2 weeks. Larval length- and weight-specific daily consumption, given as prey numbers, dry weight, and caloric value, were less for the 2/mL rotifer diet and gut residence time was longer, resulting in a higher gross growth efficiency (0.46) than the 25/mL rotifer diet (0.37). Daily percent increases in dry weight for northern anchovy fed rotifers were 15% at the low density and 21% at the high density. Northern anchovy grew the most, 23% per day, when fed 2/mL copepods, but their length-specific weight was less than those fed on the rotifer diets. Equations for the rotifer and copepod diets are given for calculating growth in length and weight, size-specific stomach contents related to feeding period, and daily food consumption based on empirically determined gastric evacuation rates. Respiration was measured directly and indirectly, by using a starvation analysis to measure the caloric equivalent of metabolism; results from both methods agreed. A power equation was used to express metabolism as a function of dry weight. Estimates of gross growth efficiencies showed that larval northern anchovy may exhibit a high growth rate or a high efficiency, but not both at the same time. Information also is given on increase in size of prey selected as northern anchovy larvae grow.

Measurements of gross-growth efficiency (calories of growth/calories consumed) of fishes are a good indicator of the adequacy of their diet and state of health (Brett and Groves 1979). Generally a favorable environment for larval fish growth can be inferred by using information on growth efficiencies as related to prey densities. A high-growth efficiency is the result of efficient assimilation of food energy for growth, with relatively little energy lost as feces or used in respiration.

A wealth of information is available on larval northern anchovy, *Engraulis mordax*. Research has been directed toward understanding the factors that affect their survival, yet no information exists on the growth efficiency of larval northern anchovy.

Larval northern anchovy have been cultured in the laboratory, and their growth and survival on wild plankton (Kramer and Zweifel 1970; O'Connell and Raymond 1970) and on cultured foods (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976) have been described and compared with their growth in the field (Methot and Kramer 1979). Incubation times, yolk absorption and the onset of feeding (Lasker 1964; Lasker et al. 1970), feeding success and swimming behavior (Hunter 1972) and their ability to withstand starvation (Hunter 1976; Theilacker and Dorsey 1980) have been studied. Here I describe how variations in prey density affect consumption, growth, and gross growth efficiencies and compare my results to those on other larval fishes.

MATERIALS AND METHODS

The rationale for my experimental design was to avoid known problems that affect interpretation of results of energetic studies. Mainly I determined gut contents directly, which gives a measure of individual variability, rather than by controlling prey level in the tank and estimating feeding by difference in prey numbers over time. To obtain more precise fresh dry weight values for these small larvae, I grouped them by size class to increase the measured weight. I converted the number of prey eaten to width-specific and species-specific fresh dry weights and caloric values, thus precluding problems inherent with feeding rate estimations that use preserved sample weights and/or average prey weights. Because gastric evacuation depends on feeding rates, I conducted the evacuation experiments with actively feeding larvae. In addition, I compared and validated traditional oxygen uptake measurements with a starvation analysis used to estimate the caloric equivalent of metabolism.

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Larval Rearing

Northern anchovy eggs were spawned by administering hormone injections to a brood stock held at the Southwest Fisheries Center (Leong 1971). Larvae raised from the eggs were kept in 100 L circular, black polypropylene tanks at constant temperature (15.5°C) and photoperiod (12 h/12 h). In this study, I varied the prey type and density. At the onset of feeding, northern anchovy larvae have small mouths that restrict their feeding to small prey (Hunter 1977). Thus for the initial feeding (day 3) all larvae were fed *Gymnodinium splendens*, a naked dinoflagellate having a width of about 50 μm (Lasker et al. 1970), and 2 days later the larvae were fed larger prey. Because it is impossible to quantify the caloric input from *Gymnodinium* directly (digested cells cannot be counted), the experiments began on day 5 when the larger prey could be removed from the fish stomachs, counted, measured, and subsequently expressed as caloric input.

Experimental Design

I conducted five experiments. In the first experiment, rotifers, *Brachionus plicatilis*, at a density of 35/mL were fed for 20 days, and the number of prey eaten was determined. The size of the rotifers was not measured in this initial experiment, but in subsequent experiments, widths of prey eaten were measured. In the second and third experiments, rotifers were offered at densities of 2 and 25/mL respectively for 14 days. In the fourth experiment, copepods, *Tigriopus californicus*, nauplii and copepodites were fed to larvae at a density of 2/mL (usually 1 nauplius and 1 copepodite/mL) for only 9 days instead of 14 days because of problems with the copepod culture. In the fifth experiment, larvae were fed copepods at 0.2/mL for 12 days without the initial addition of *Gymnodinium*. (Mortalities were high on this low density copepod diet, and data are few; high mortalities are consistent with results reported by O'Connell and Raymond [1970] for northern anchovy raised on a similar diet. The addition of a *Chlorella* bloom to this diet improves survival of northern anchovy [Moffatt 1981].)

To estimate larval growth as the increase in standard length, SL, and dry weight, W, larvae were pipetted individually onto a slide and measured while alive. Larvae were then rinsed in distilled water and, to ensure dependable mean dry weight determinations, grouped by size class onto a clean slide. Larvae <5 mm were grouped by 0.2 mm size class, and those >5 mm were grouped by 0.3 mm size class. Numbers of larvae per group ranged between 2 and 12; the larger the larval weight, the fewer larvae I grouped together. After drying to a constant weight at 60°C (Lovegrove 1966), larvae were removed from the slides by using a single-edged razor blade and weighed on a Cahn electrobalance to ±2 μg.

Feeding

To estimate feeding rates and daily consumption, each prey item removed from the larva's gut was counted and its width measured. Width is the dimension that limits a fish larva's selection of prey (Beyer 1980; Hunter 1981). Prey defecated onto the slide were included in the total number eaten. Gut contents in dry weight were determined by summing the width-specific weights of the prey eaten each day. I used the width-specific fresh dry weights and caloric values for *Brachionus* and *Tigriopus* given by Theilacker and Kimball (1984) and reproduced here in Table 1.

Because northern anchovy larvae eat continuously, asymptotic curves ($c = C_{max} \times (1 - e^{-kt})$) were used to describe food intake, i.e., the relation between observed gut contents c and time t, where C_{max} is the asymptotic gut contents (contents in gut at steady state after filling) and k is the instantaneous rate of gut filling. Using Marquardt's algorithm for fitting nonlinear models, parameters C_{max} and k were estimated for 0.5 mm length classes (Table 2). Fish with empty stomachs were included in this analysis because all fish were used in the growth estimates. Daily mean gut contents $\bar{c}$ were calculated by integrating the area beneath

TABLE 1.—Width-specific dry weight and caloric value of rotifers, *Brachionus plicatilis*, and copepods, *Tigriopus californicus*[1].

Prey	Width class μm	Per individual: Dry weight μg (SE)	Per individual: Volume × 10^6 μm	Per individual: Caloric value × 10^{-3} cal
Brachionus plicatilis (4.4 cal/mg)				
Rotifers	74.3-109.7	0.10 (0.01)	0.65	0.44
	109.8-146.7	0.22 (0.04)	1.73	0.97
	146.8-183.8	0.41 (0.06)	2.96	1.80
	183.9-195.0	0.47 (0.08)	3.99	2.07
Tigriopus californicus (4.9 cal/mg)				
Nauplii	74.3-109.7	0.04 (0.01)	0.20	0.20
	109.8-146.7	0.13 (0.01)	0.55	0.64
	146.8-183.8	0.25 (0.01)	1.17	1.23
	183.9-195.0	0.38 (0.00)	1.77	1.86
Copepodites	146.8-183.8	0.63 (0.15)	3.38	3.09
	183.9-221.0	1.20 (0.26)	6.21	5.88

[1]From Theilacker and Kimball 1984, table 2.

TABLE 2.—Estimates of the asymptotic gut contents (C_{max}) and instantaneous rate of gut filling (k) for northern anchovy (n) fed several diets[1].

Diet	Prey level per mL	SL (mm)	n	Prey number C_{max}	Prey number k	Prey weight µg C_{max}	Prey weight µg k
Rotifers[2]	35	4.00	89	6.16	0.33		
		5.00	236	9.90	0.32		
		6.00	131	11.91	1.13		
		7.00	219	15.92	3.73		
		8.00	159	28.33	3.78		
		9.00	171	46.36	2.56		
		10.00	89	52.22	1.72		
Rotifers	25	4.25	58	[3]15.55	0.12	1.80	0.29
		4.75	69	7.79	0.67	2.12	0.67
		5.25	54	12.93	0.62	2.36	0.83
		5.75	35	14.01	0.64	2.92	0.58
		6.50	28	16.97	1.96	3.31	3.76
		8.00	32	27.80	1.84	6.68	1.61
Rotifers	2	4.25	33	7.44	0.35	0.50	0.18
		4.75	19	4.97	1.61	1.35	0.98
		5.25	18	8.86	1.29	2.42	0.73
		8.00	16	9.94	1.30	4.00	0.88
Copepods[4]	2	4.25	21	1.54	1.27	0.08	0.49
		4.75	63	4.89	0.42	0.52	0.37
		5.25	44	4.45	0.45	0.94	0.57
		5.75	32	3.86	0.41	1.15	1.49
		[5]6.25	31	4.94	1.01	1.99	0.88
		8.00	14	7.22	1.30	3.66	0.66

[1]Includes zero gut contents; observed gut contents c at time t = $C_{max} \times (1 - e^{-kt})$.
[2]Prey width not measured.
[3]87% rotifers <150 µm width.
[4]Fish eating *Gymnodinium* exclusively were removed to estimate C_{max} and k.
[5]Copepod concentration <0.1/mL.

the curves and dividing by the 12-h feeding period.

Equations were derived for each diet from the relation of C_{max} and k with fish size and duration of feeding; these equations allow the calculation of gut contents c at time t for all fish lengths between 4 and 8 mm. The parameters (Table 3) were found using the derivative-free nonlinear regression program (BMDPAR) by Biomedical Computer Programs (BMDP, 1981).

Daily consumption F_w was estimated using a modification of an equation for consumption developed by Stauffer (1973) and discussed by Elliott and Persson (1978) and Jobling (1981), $F_w = rt + C_{12}$, where r is the µg evacuated per hour calculated as mean gut contents $\bar{c}$ divided by the empirically determined rate of gastric evacuation (see Evacuation Rates), t is the duration of feeding, and C_{12} is the dry weight of the food remaining in the stomach at the end of the 12-h feeding period.

Growth

Length data for all feeding treatments were fit to exponential growth curves, $SL = l_0 e^{kt}$ where l_0 is length at hatching, k is the instantaneous growth rate and t is the age. Length-weight data were fit to a power equation where weight $W = a(SL)^b$; parameters for the growth equations are given in Table 4.

TABLE 3.—Parameters for equation[1] relating observed gut contents c in µ g dry weight at time t to standard length (SL) of northern anchovy fed three diets.

Diet	Age	n	P_1	(SD)	P_2	(SD)	P_3	(SD)	P_4	(SD)
Rotifers										
25/mL	5-14	280	−1.90	(0.70)	0.51	(0.18)	0.57	(0.16)	0.29	(0.03)
2/mL	5-14	103	—	—	[2]0.69	—	0.33	—	0.326	—
Copepods										
2/mL	5-9	171	2.84	(0.88)	−0.39	(0.12)	[3]1.26	[3](0.75)	1.18	(0.10)

[1]$c = p_3 e^{p_4 SL(1 - e^{-(p_1 + p_2 * SL)t})}$.
[2]$(P_1 + P_2)$ fixed at 0.69, the mean k from Table 2; asymptotic standard deviations could not be computed because k was held constant.
[3]$\times 10^{-3}$.

TABLE 4.—Parameters for northern anchovy growth equations where SL is standard length in mm, W is weight in µg, and t is age in days.

Diet	Age (d)	Age length $SL = l_0 e^{kt}$ n	l_0	(SD)	k	(SD)	Length-weight $W = a(SL)^b$ n	a	(SD)	b	(SD)
Rotifers											
25/mL	5-14	280	3.06	0.05	0.06	0.001	253	0.197	0.040	3.16	0.11
2/mL	5-14	103	3.14	0.07	0.05	0.002	84	0.379	0.030	2.80	0.04
Copepods											
2/mL	5-9	138	3.06	0.15	0.07	0.010	109	0.297	0.097	2.88	0.20

Metabolism

I determined metabolic rates for the larvae, which ranged in age from first-feeding (3 days after hatching) to 25 days using the Winkler technique. I chose the Winkler technique where large vessel volumes could be used and there was no need to shake the vessels during the experiment, as required for manometric techniques. Pearcy et al. (1969) found no differences between Winkler and Warburg estimates of oxygen consumption. Oxygen consumption was estimated at 16°C during 18-23 h experimental periods with a 12 h light-dark cycle. The respiration vessels were attached to a large, slowly rotating wheel. Young larvae, 0.02-0.14 mg dry weight were tested in 40 mL vessels in groups of 10-50, while larvae older than 16 days (larger than 0.14 mg) were tested individually in 60-150 mL vessels. All fish tested had empty guts. Data were not used when mortalities occurred during the experiment.

To express metabolism (Q) as a function of dry weight, I used a nonlinear regression to fit a power equation to the data (see parameters for Model 1 in Table 5). The data points were weighted by their sample size (n = 10-50). The Model 1 fit was unsatisfactory for the whole size range, presumably because each data point for the young larvae (n = 72) was a group mean, and the model was significantly weighted toward the young larvae, causing it to overestimate oxygen consumption for the few large larvae (n = 17). Because the experimental technique differed (i.e., respiration was measured for groups of young larvae or individual older larvae), I also fitted two separate curves. These curves (Model 2) gave a good fit to the data (Table 5); the Model 2 equation for younger larvae was used in the present study.

An alternate approach for estimating metabolic requirements is to starve larvae of known size (weight), determine the size-specific weight loss, and convert the weight loss to calories. This approach eliminates the need to restrict larval swimming activity in a respiration vessel. Presumably the weight loss in caloric units would equal the loss due to metabolic costs, excluding the metabolic cost of attacking prey. Using this approach, I fed control northern anchovy larvae ad libitum on *Gymnodinium* and *Brachionus* and starved the test larvae; both groups were maintained in 100 L rearing tanks at 15.5°C. Live standard length and dry weight of groups of the same length were measured daily, as described earlier in this Methods section, for 10-50 larvae sampled daily from each treatment.

I calculated the caloric equivalent of northern anchovy tissue using the caloric values given by Hunter and Leong (1981) for fat-free anchovy tissue, 4.129 cal/mg, and for anchovy lipid, 9.227 cal/mg. For example, northern anchovy larvae weighing 25 μg contained 6 μg of lipid (unpubl. data: John Hakanson, UCSD, Scripps Institution of Oceanography); using the above caloric equivalents for 19 μg of fat-free tissue and 6 μg of lipid yields 5.36 cal/mg as the energy equivalent of anchovy tissue. In a 20-d laboratory experiment, Hakanson found that lipid weight appeared to increase proportionally with anchovy weight, thus the caloric content of anchovy tissue would be approximately constant for the age range studied. Lipid content seems to be lower in older northern anchovy larvae. The only other information I found was for 40-60 d-old northern anchovy where the caloric content averaged 4.9 cal/mg (unpubl. data: John Hunter, Southwest Fisheries Center). I used 5.4 cal/mg as the caloric value of anchovy tissue for larvae between 5 and 14 days of age.

TABLE 5.—Parameters for equation $Q = aw^b$ where Q is metabolic rate in μL O_2/h for northern anchovy and w is their fresh dry weight.

Model	N	Size group (mg dry wt) w	Parameters a(SE)	b(SE)
1	89	0.02-2.70	[1]3.844 ± 0.100	0.858 ± 0.029
2	72	0.02-0.14	2.897 ± 0.344	0.834 ± 0.057
2	17	0.14-2.70	4.269 ± 0.325	0.697 ± 0.107

[1]The sum of the residuals in Model 1 does not equal zero, thus the program calculation of SE's is biased.

Evacuation

Gut clearance times were determined for actively feeding fish of various ages fed the rotifer and copepods diets. Larvae were transferred from the 100 L rearing tank to a 10 L test tank. Because northern anchovy larvae are sensitive to handling, handling was restricted to one transfer. Transferred larvae were kept in the test tank for 18 hours prior to an evacuation experiment because injured larvae usually die within 8-10 hours after transfer. First, larvae were fed a low concentration of prey that had been dyed with National Fast Blue (Laurence 1971). After larvae had filled their guts, eating most of the dyed prey, a known density of undyed prey was added. Larvae were sampled at 5-min intervals, and the time required for them to void their guts of the dyed prey was determined. The number of prey in the full guts was counted and converted to dry weight. Evacuation rates are given as μg prey cleared through the gut per hour. Rates were related to fish size and to prey type.

The timing of the second prey addition was not critical for determining gut clearance rates at high prey densities. But when the timing was not correct for the tests that used low prey concentrations, deciphering the meaning of the gut contents was problematical. Results from most of these low-density tests could not be used.

A series of evacuation experiments also was conducted with nonfeeding northern anchovy that were removed from their food source, rotifers, to filtered seawater.

To reduce the incidence of injury during transfer, I constructed a cylindrical, clear plastic container (15 mm high and 7 mm diameter) with handle and a removable bottom grooved to fit the circumference of the cylinder. Larvae to be transferred were surrounded by the cylinder, and then the bottom was fitted onto the cylinder. The container with fish was transferred and lowered into the test tank. Removing the bottom and slowly raising the cylinder released the fish. Prey that were transferred into the experimental tank with the larvae were removed by an air-lift pump that slowly recirculated water and was screened to prevent the removal of larvae (O'Connell and Paloma 1981).

Growth Efficiency

To determine growth efficiencies, I used the information on growth (Table 4), daily food consumption estimated from the general equations (Table 3) and evacuation rates of 1.15 hours for the high-density rotifer diet and 1.5 hours for the low-density diet. Gross growth efficiency was estimated based on dry weight and on caloric estimates. It is the ratio of growth to ingestion. To estimate assimilation efficiency, I used the information on weight-specific metabolic rates and simply combined the energy of metabolism and growth and divided it by the energy consumed. Assimilated energy lost as feces and urine was not accounted for.

RESULTS

Feeding

Sizes of prey fed to larval northern anchovy in these experiments ranged from 50 μm for *Gymnodinium*, to 74-195 μm for rotifers and copepod nauplii, and 147-221 μm for copepodites. In contrast to larvae fed the rotifer diets, fish offered the copepod diet did not switch from eating *Gymnodinium* at first feeding on day 3 to eating larger prey on day 5. All fish fed copepods and sampled on day 5 contained *Gymnodinium* in their gut, and 96% of these guts were full of *Gymnodinium* (Table 6). By day 7, the number of copepod-fed northern anchovy eating *Gymnodinium* had decreased to 80%, with 10% full. These data reveal that young northern anchovy were unsuccessful at capturing *Tigriopus* nauplii at 1/mL until 7-8 days of age, and because of this behavior and the failure of the copepod culture on day 9, I was unable to quantify daily consumption for northern anchovy fed copepods.

Northern anchovy reared on the low-density (2/mL) and high-density (25/mL) rotifer diets ate only a few *Gymnodinium* cells after day 4. Between rotifer treatments, incidence of feeding on *Gymnodinium* after day 4 was higher for fish fed the low-density diet (Table 6). On day 5, northern anchovy concentrated on eating rotifers in the 75-150 μm size range; between 84 and 97% of the rotifers eaten by larvae sampled from both rotifer treatments were <150 μm width (Table 7). Only 7% of the rotifers available to these larvae were smaller than 150 μm width. Hence on day 5 larvae were selecting small rotifers in higher proportions than were available; in the two treatments, the apparent density of roti-

TABLE 6.—Presence of *Gymnodinium* in guts of larval northern anchovy related to age of larvae and to diet.

	Diets								
	Rotifers 25/mL[1]			Rotifers 2/mL[2]			Copepods 2/mL[3]		
Age (d)	*n*	Incidence (%)[4]	Gut full (%)[5]	*n*	Incidence (%)[4]	Gut full (%)[5]	*n*	Incidence (%)[4]	Gut full (%)[5]
5	21	48	0	29	83	0	27	100	96
6	82	59	0	11	9	0	57	77	16
7	10	10	0	5	0	0	49	80	10
8	75	9	0	0	—	—	5	0	0
9	27	7	0	38	6	0	33	0	0

[1]Apparent density of rotifers <150 μm = 2/mL.
[2]Apparent density of rotifers <150 μm = 0.1/mL.
[3]Apparent density of nauplii <150 μm = 1/mL.
[4]Percent of larvae having *Gymnodinium* cells in guts with rotifers or copepods.
[5]Percent of larvae having guts full with *Gymnodinium* cells.

TABLE 7.—Width frequency of prey eaten by northern anchovy (n) related to their diets and to their age and size.

Age (d)	Rotifers 25/mL[1] Prey composition (%)			Rotifers 2/mL[2] Prey composition (%)			Copepods 2/mL[3] Prey composition (%)		
	n	<150 μm	>150 μm	n	<150 μm	>150 μm	n	<150 μm	>150 μm
5	21	83.5	16.5	29	97.3	2.7	27	88.0	12.0
6	82	11.0	89.0	11	75.0	25.0	57	60.0	40.0
7	10	5.2	94.8	5	38.7	61.3	49	59.0	41.0
8	75	33.1	66.9	0	—	—	5	33.4	56.6
9	27	40.9	59.1	38	12.2	87.8	33	31.8	68.2
Length (mm)									
4.1-4.5	60	49.7	50.3	37	91.4	8.6	21	80.0	20.0
4.6-5.0	77	25.7	74.3	20	23.4	76.6	69	68.3	13.7
5.1-5.5	55	43.9	56.1	23	15.1	84.9	45	57.3	42.7
5.6-6.0	35	36.6	63.4	9	11.8	88.2	30	40.0	60.0
6.1-6.5	23	38.2	61.8	0	—	—	17	36.4	63.6

[1]Apparent density of prey <150 μm = 2/mL.
[2]Apparent density of prey <150 μm = 0.1/mL.
[3]Apparent density of prey <150 μm = 1/mL.

fers <150 μm was equivalent to about 2 and 0.1/mL. In sum, the larvae switched to eating prey >150 μm on day 6 in the high-density rotifer treatment, day 7 in the low-density treatment, and day 8 in the copepod treatment (Table 7). If the analysis is based on larval size instead of larval age, selection for prey >150 μm occurs at 4.6-5.0 mm for northern anchovy fed the rotifer diets and at 5.6-6.0 mm for those fed the copepod diet (Table 7; Fig. 1).

Feeding intensity was highly variable on all diets. The observed stomach contents can differ by as much as a factor of three (Fig. 2) from the predicted stomach contents (C_{max}) used in the feeding models.

At high rotifer densities, northern anchovy filled their guts at a faster rate and consumed more. On average, fish eating the high-density rotifer diet were full within 2 hours, while those eating a low-density diet were full in about 3 hours. Comparing the average observed stomach contents, and excluding empty stomachs, for fish of equal age shows that all larvae eating at the high prey density ate more than their counterparts eating at lower prey densities (Table 8).

Growth

Hunter (1976) showed that the length-weight rela-

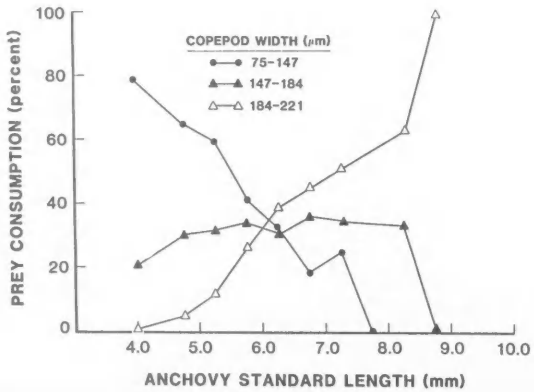

FIGURE 1.—Size of copepod prey eaten by northern anchovy related to fish size. See Table 1 for copepod width classes.

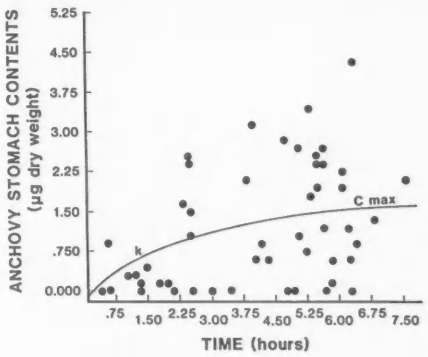

FIGURE 2.—Observed stomach contents of 4.0-4.5 mm northern anchovy fed 25 rotifers/mL, predicted rate of gut filling k and predicted maximum gut content C_{max}. Each point is one larva.

TABLE 8.—Mean dry weight of food (µg) observed in stomachs[1] of northern anchovy (n) related to their age.

Age	Rotifers 25/mL		Rotifers 2/mL		Copepods 2/mL		Copepods 0.2/mL	
(d)	n	µg	n	µg	n	µg	n	µg
5	9	1.75	17	0.60	8	0.18		
6	57	2.23	4	0.27	39	0.55		
7	8	3.56	5	1.41	37	0.67		
8	51	2.10	—	—	3	0.87	1	0.08
9	26	2.99	27	2.60	31	1.88	6	0.78
10	—	—	—	—			9	1.51
11	6	3.60	—	—			9	0.42
12	22	5.14	4	[2]6.39			3	0.90

[1]Average stomach contents (excludes empty stomachs) calculated for t = >3 hours; 3 hours is a reasonable time for northern anchovy to fill guts eating at lowest prey densities tested (see text).
[2]Day 13.

tion for northern anchovy was curvilinear on a log-log plot, and he used a Laird Gompertz model to describe both growth in length and in weight over 75 days. Because I am describing only the first 2 weeks of growth, I used a simpler exponential model (Table 4) which probably should not be used for larvae beyond 2 weeks of age.

Larvae grew at 0.35 mm/day on the copepod diet (k = 0.07) and at 0.33 and 0.25 mm/day on the high- (k = 0.06) and low-density (k = 0.05) rotifer diets (Table 4). On the average, the dry weight of larval northern anchovy was proportional to length to the third power. Depending on diet, the length exponent ranged from 2.80 to 3.16 (Table 4).

Daily percent increases in dry weight for northern anchovy fed the rotifer diets were 15% for larvae fed 2/mL and 21% for larvae fed 25/mL. However, northern anchovy grew the most, 23% per day, on the 2/mL copepod diet. For the three diets tested, daily growth in dry weight as a percent was constant over the size range.

An analysis of covariance was used to test for diet-induced differences in the relation between natural logarithms of length and weight for larval northern anchovy between days 5 and 9 when prey concentrations were controlled. Larvae which fed on copepods were significantly longer and heavier at age than larvae eating rotifers. There were no length or weight differences at age 7 days between the two rotifer treatments (Table 9), but there were differences in growth thereafter. Larvae raised on the two rotifer diets were the same weight at 4.9 mm (30.75 and 33.25 µg; P = 0.3), but larvae raised on copepods weighed less at 4.9 mm (28.54 µg) than larvae fed on the rotifer diets (P = 0.11 and <0.01).

I compared the distribution of my northern anchovy dry weights at length for the rotifer and

TABLE 9.—Effect of diet on northern anchovy standard length (SL) and dry weight (W).

Diet	Density per mL	No. cases[1]	Age = 7 days $\bar{x}$ SL (mm)	$\bar{x}$ W (µg)	Probabilities = SL and = W 1 vs. 2 SL/W	1 vs. 3 SL/W	2 vs. 3 SL/W
1-Rotifers	25	34	4.78	28.36	0.20/0.71	0.00/0.00	0.00/0.00
2-Rotifers	2	14	4.61	27.33			
3-Copepods	2	28	5.28	35.11			

			SL = 4.9 mm $\bar{x}$ W (µg)	Probabilities 1 vs. 2	1 vs. 3	2 vs. 3
1-Rotifers	25	34	30.75	0.30	0.11	0.00
2-Rotifers	2	14	33.25			
3-Copepods	2	28	28.54			

[1]Case numbers contain 2-12 larvae depending on number in group that were weighed.

copepod diets with those in a study by Hunter (1976) where northern anchovy were fed *Brachionus*, 50-100/mL, and copepods, *Tisbe* 0.01/mL, at 17°C and *Gymnodinium* was fed as the first food. The curves show that among experiments there appear to be diet-induced differences in weight at length (Fig. 3).

Metabolism

The caloric equivalent of metabolism for northern anchovy larvae ranging in age from first feeding to 25 days was determined using the relation between the metabolic rate and fresh dry weight (Model 2, Table 5) and by converting the oxygen uptake to calories using an oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves 1979). I assume the metabolic rate approximates "routine" metabolism.

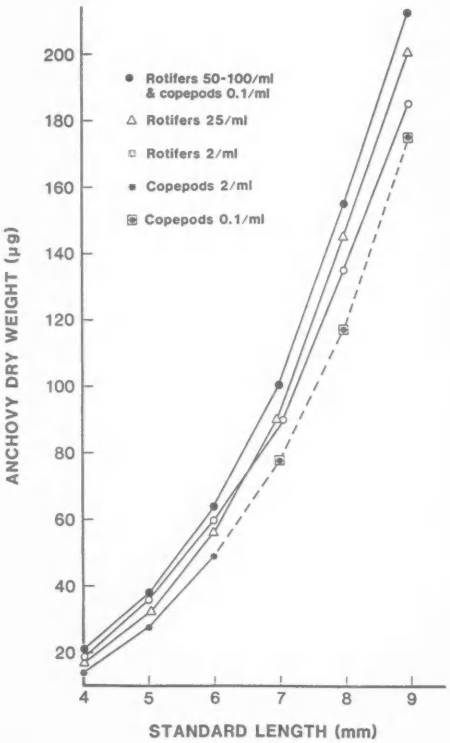

FIGURE 3.—Relation between dry weight and standard length for northern anchovy fed several diets where *Gymnodinium* was the first food.

I also determined the caloric equivalent of metabolism for first-feeding northern anchovy by starving them, determining the weight loss, and converting the loss to calories. Starving larvae lost an average of 10% of their body weight per day for 3 days, after which larvae must have continued to lose weight, but no decrease could be measured (Fig. 4). The time to maximum weight loss was 3-4 days, the time of irreversible starvation for northern anchovy from the onset of feeding (Lasker et al. 1970; Theilacker and Dorsey 1980). Larvae that weighed an average of 0.0211 mg at 3 days of age weighed an average of 0.0148 mg on day 6. The weight loss (0.0063 mg) $\times$ 5.4 cal/mg, which is the assumed caloric equivalent for northern anchovy tissue, equals 0.0339 calories, or a metabolic demand of 0.011 cal/day. This value, determined at a slightly lower temperature, corresponds well with the value obtained for first-feeding northern anchovy weighing 0.0211 mg using respiration measurements (0.013 cal/day).

Evacuation Rates

Gut clearance times for northern anchovy larvae appeared to be independent of larval age; however, the weight of food evacuated per hour increased with age because the stomach contents increased. Because the larvae fed at a constant rate after the gut was filled and defecated continuously, the gut clearance rate for actively feeding northern anchovy larvae was constant. The average gut clearance time for anchovy feeding on 25 rotifers/mL was 1.15 hours (SE = 0.13; range 0.7-1.5 hours; n = 6 tests). Reducing the prey density to 2/mL increased the average gut clearance time to 1.5 hours (range 1.2-1.8 hours; n = 2 tests) for the rotifer diet and 2.73 hours (SE = 0.26; range 2.0-3.3 hours; n = 4 tests) for the copepod diet.

Nonfeeding northern anchovy cleared their guts in 2.8-5.8 hours, depending on their size and stomach capacity (2.8 h/4.8 mm; 4 h/6.3 mm; 5 h/7.9 mm; 5.8 h/8.5 mm).

Daily Consumption of Rotifers and Growth Efficiency

Daily consumption was less on the low-density diet and, as a percent of body weight eaten per day, consumption ranged between 31 and 86%, depending on prey concentration and fish size (Tables 10, 11). For both rotifer diets, weight-specific consumption decreased with increasing body weight (Fig. 5).

Gross growth efficiencies were higher for north-

ern anchovy fed the low-density diet (Tables 10, 11). Mean gross-growth efficiency (days 5-14) based on dry weight was 0.30 for the high-density diet and 0.37 for the low-density diet. Based on calories, mean gross-growth efficiencies were 0.37 and 0.46 respectively.

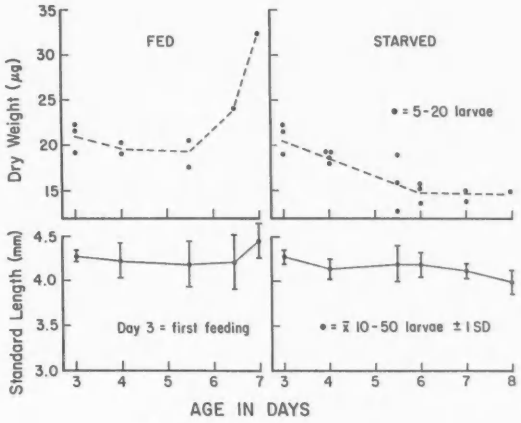

FIGURE 4.—Changes in standard length and weight of fed and starved northern anchovy larvae over time.

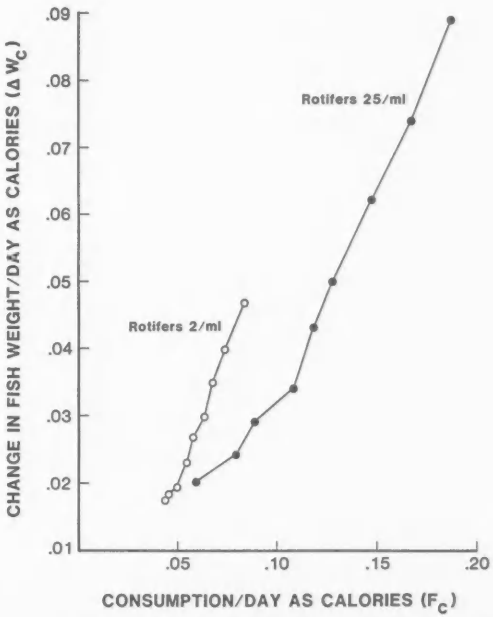

FIGURE 5.—Gross growth efficiencies (W_c/F_c; Tables 10, 11) of northern anchovy fed rotifers at 25/mL and at 2/mL.

TABLE 10.—Estimation of growth efficiency of larval

Diet	Age (d) A	Standard length (mm) l	Dry weight (μg) W	Gut clearance rate (μg/h) r	Gut contents: Daily mean (μg) $\bar{c}$	Gut contents: Residual at end of feeding (μg) C_{12}	Consumption: Food (μg) F_w	Consumption: Body weight (%/d) $F_{w/W}$	Co
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	
Rotifers (25/mL)	5	4.13	17.41	1.03	1.19	1.73	14.14	81	
	6	4.39	21.12	1.34	1.54	2.00	18.11	86	
	7	4.66	25.50	1.58	1.82	2.19	21.14	83	
	8	4.95	30.86	1.80	2.07	2.39	23.99	78	
	9	5.25	37.17	2.03	2.33	2.61	26.97	73	
	10	5.58	45.06	2.28	2.62	2.88	30.23	67	
	11	5.92	54.33	2.55	2.94	3.17	33.82	62	
	12	6.29	65.80	2.88	3.31	3.53	38.04	58	
	13	6.68	79.57	3.25	3.74	3.96	42.94	54	
	14	7.09	96.05	3.68	4.24	4.45	48.67	51	

[1]Hatching = Day 0.

[2]$l_t = 3.06\, e^{0.06\, t}$; live length.

[3]$W = 0.197\, l^{3.16}$ (on day consumption is estimated); fresh dry weight.

[4]$r = \bar{c}/1.15$ h (see text).

[5]$\bar{c} = \int_0^{12} C_{max}\,(1 - e^{-kt})/12 \cdot dt$.

[6]$C_{12} = C_{max}\,(1 - e^{-12\,k})$.

[7]$F_w = rt + C_{12}$; t = 12 h.

[8]$F_{w/W}$.

[9]$F_c = F_w \times 4.$

[10]μL O_2/d = 24

[11]Q_m 0.00463 ×

[12]ΔW = weight

[13]$\Delta W_c = \Delta W \times$

[14]$\Delta W / F_w$.

[15]$\Delta W_c / F_c$.

[16]$P = \dfrac{Q_m + \Delta}{F_c}$

larval northern anchovy fed rotifers at 25/mL.

)	([9])	([10])	([11])	([12])	([13])	([14])	([15])	([16])
umption								
dy ght /d)	Calories (cal/d)	Metabolic rate (μL O_2/d)	(cal/d)	Change in fish weight (μg/d)	(cal/d)	Gross efficiency		Assimilation estimate
/w	F_c		Q_m	ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$	P
1	0.06	2.36	0.010	3.71	0.020	0.26	0.33	50.2
6	0.08	2.77	0.012	4.38	0.024	0.24	0.30	44.4
3	0.09	3.24	0.014	5.35	0.029	0.25	0.32	47.5
8	0.11	3.80	0.016	6.31	0.034	0.26	0.31	45.7
3	0.12	4.44	0.019	7.89	0.043	0.29	0.36	51.3
7	0.13	5.21	0.022	9.27	0.050	0.31	0.38	55.6
2	0.15	6.09	0.026	11.48	0.062	0.34	0.41	58.7
8	0.17	7.14	0.031	13.77	0.074	0.36	0.44	61.7
4	0.19	8.37	0.036	16.48	0.089	0.38	0.47	65.7
1	0.21	9.79	0.042					

F_w = 4.4 cal/mg (see Table 1).
/d = 24 (2.879 $W^{0.834}$) (see Table 5).
00463 × μL O_2/d; (1 μL O_2 = 0.00463 cal) (see text).
weight gained 1 day after consumption estimated.
= ΔW × 5.4 cal/mg (caloric estimation for larva) (see text).

$$\frac{}{c}$$

$$\frac{m + \Delta W_c}{F_c}.$$

TABLE 11.—Estimation of growth effici

Diet	Age (d) A	Standard length (mm) l	Dry weight (μg) W	Gut clearance rate (μg/h) r	Gut contents: Daily mean (μg) $\bar{c}$	Gut contents: Residual at end of feeding (μg) C_{12}	Foo (μ $F_$
	(1)	(2)	(3)	(4)	(5)	(6)	(7
Rotifers (2/mL)	5	4.03	18.77	0.72	1.08	1.23	9.
	6	4.24	21.64	0.76	1.15	1.31	10.
	7	4.46	24.93	0.83	1.24	1.41	11.
	8	4.68	28.53	0.89	1.33	1.52	12.
	9	4.92	32.82	0.96	1.44	1.64	13.
	10	5.18	37.19	1.05	1.57	1.79	14.
	11	5.44	43.48	1.14	1.71	1.94	15.
	12	5.72	50.04	1.25	1.87	2.13	17.
	13	6.01	57.48	1.37	2.06	2.34	18.
	14	6.32	66.17	1.52	2.28	2.59	20.

[1]Hatching = Day 0.

[2]$l_t = 3.14\, e^{0.05\, t}$; live length.

[3]$W = 0.379\, l^{2.80}$ (on day consumption is estimated); fresh dry weight.

[4]$r = \bar{c}/1.5$ h (see text).

[5]$\bar{c} = \int_0^{12} C_{max}\,(1 - e^{-kt})/12 \cdot dt$.

[6]$C_{12} = C_{max}\,(1 - e^{-12k})$.

[7]$F_w = rt + C_{12}$; t = 12 h.

[8]$F_{w/W}$.

th efficiency of larval northern anchovy fed rotifers at 2/mL.

	[7]	[8]	[9]	[10]	[11]	[12]	[13]	[14]	[15]	[16]
	Consumption					Change in fish weight				
al of g	Food (μg)	Body weight (%/d)	Calories (cal/d)	Metabolic rate (μL O_2/d)	(cal/d)	(μg/d)	(cal/d)	Gross efficiency		Assimilation estimate
	F_w	$F_{w/W}$	F_c		Q_m	ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$	P
	9.87	53	0.043	2.50	0.012	2.87	0.015	0.29	0.35	67.3
	10.51	49	0.046	2.83	0.013	3.29	0.018	0.31	0.39	66.6
	11.33	45	0.050	3.18	0.015	3.60	0.019	0.32	0.38	68.4
	12.16	43	0.054	3.56	0.016	4.29	0.023	0.35	0.43	74.0
	13.16	40	0.058	4.00	0.019	5.09	0.027	0.39	0.47	79.3
	14.35	38	0.063	4.51	0.021	5.57	0.030	0.39	0.48	80.6
	15.62	36	0.069	5.06	0.023	6.56	0.035	0.42	0.51	85.5
	17.09	34	0.075	5.68	0.026	7.44	0.040	0.44	0.53	88.3
	18.82	33	0.083	6.38	0.030	8.69	0.047	0.46	0.57	92.2
	20.83	31	0.092	7.18	0.033					

[9] $F_c = F_w \times 4.4$ cal/mg (see Table 1).

[10] μL O_2/d = 24 (2.879 $W^{0.834}$) (see Table 5).

[11] Q_m 0.00463 × μL O_2/d; (1 μL O_2 = 0.00463 cal) (see text).

[12] ΔW = weight gained 1 day after consumption estimated.

[13] $\Delta W_c = \Delta W \times 5.4$ cal/mg (caloric estimation for larva) (see text).

[14] $\Delta W/F_w$.

[15] $\Delta W_c/F_c$.

[16] $P = \dfrac{Q_m + \Delta W_c}{F_c}$.

DISCUSSION

Larval northern anchovy feeding ecology was similar to other larval fishes (Laurence 1977; Haegler and Outran 1978; Werner and Blaxter 1980; Theilacker and Dorsey 1980; Blaxter and Hunter 1982; Eldridge et al. 1982; Houde and Schekter 1981, 1983). As the larval northern anchovy grew they selected increasing larger prey, and on the rotifer diets, their feeding and growth rates increased with increasing concentrations of prey. In addition to the growth response to different prey concentrations, I observed differences in growth due to prey type. Fish grew the fastest on the copepod diet where one-third fewer calories were available than were available in the high-density rotifer diet ($4 \times 10\text{-}2$ vs. $13 \times 10\text{-}2$ cal/mL for prey <150 μm).

Length at age obtained for the first 2 weeks by larvae raised on copepods agreed with previous studies where northern anchovy were fed copepods and *Gymnodinium* was the first food (Kramer and Zweifel 1970; Hunter 1976). However, the larvae raised on copepods did not put on as much weight per unit length as their counterparts fed rotifers and *Gymnodinium*. Between days 5 and 9, the faster growing, copepod-fed larvae had significantly lower size-specific weights, and the weight exponents estimated for the first 2 weeks were lower, 2.9, than for larvae feeding on the high-density rotifer diet, 3.2. Lasker et al. (1970) found an exponent of 3.3 for northern anchovy fed on a high-density veliger and *Gymnodinium* diet.

These weight exponents estimated for northern anchovy are lower than the exponents of about 4 reported for deep-bodied fish larvae (haddock, flounder, cod, and scup; Laurence 1979). Likewise the exponents obtained for Atlantic herring ranged between 3.8 and 4.7 (reviewed by Checkley 1984). Weights of fishes used to estimate the exponents in the other laboratory studies ranged between 20 and 10,000 μg, whereas the northern anchovy weights ranged between 20 and 100 μg. Differences in growth rates occur as larval fish grow (Zweifel and Lasker 1976), and length-weight relations may change over the size range. Additionally, larval morphology is an obvious important component in the length-weight relation, and experimental variables may further complicate the relation. Moksness (1982) reported a low weight exponent of 2.6 for capelin, *Mallotus villosus*, from the field and from a large rearing basin. Both Atlantic herring and capelin larvae are similar in morphology to northern anchovy.

In previous laboratory feeding studies of larval northern anchovy, percent of body weight eaten per day was usually higher than consumption rates, 31-86%, I estimated. Reported values were 126-144% for northern anchovy (Hunter 1972), 197-440% for bigeye anchovy (Chitty 1981), and 20-295% for bay anchovy (Houde and Schekter 1981). Consumption varies with prey concentration and temperature, and the differences may be due to the experimental conditions. In the other studies, temperatures were higher and food concentrations were both lower and higher, with some including *Chlorella* blooms. However, it is likely that the differences are due to use of average food weights in the other studies. First-feeding northern anchovy larvae select small prey (Table 7; Fig. 1), and if average prey weight is larger than those actually being eaten by the larvae, their consumption may have been overestimated. For example, in Table 2, the average full stomach (C_{max}) of 4.25 mm fish (day 4-5) fed 25 rotifers/mL contained 15.55 rotifers while the average 4.75 mm fish (day 5-6) contained 7.79 rotifers. Using the width-specific weights (Table 1), I converted the 15 small rotifers to 1.8 μg and the 8 larger ones to 2.1 μg.

The exponent for the regression relating oxygen consumption to northern anchovy weight was 0.834 for larvae weighing <0.14 mg and 0.697 for larger larvae. Exponents have been reported for larval winter flounder, *Pseudopleuronectes americanus* (0.74; Laurence 1975); larval bay anchovy, *Anchoa mitchilli* (0.8; Houde and Schekter 1983); larval sea bream, *Archosargus rhomboidalis*, and larval lined sole, *Achirus lineatus* (0.838 and 0.942; Houde and Schekter 1983). Brett and Groves (1979) suggested a weight exponent of 0.86 for adult fish. There is considerable variation in respiration rates in the literature, probably depending on experimental conditions. The respiration rates given here for northern anchovy range between 3.1 and 6.9 μL/mg per hour for 0.02-2.7 mg larvae, and they are comparable to rates given for other fishes of similar age and size (reviewed by Theilacker and Dorsey 1980).

The evacuation rates determined here, 1.15-2.73 hours, for actively feeding northern anchovy larvae are comparable to rates of 1-3 hours estimated by Arthur (1976) for field samples. Particle residence time in the gut depended on prey density, prey type, and experimental design, e.g., feeding vs. nonfeeding larvae. Werner and Blaxter (1980) also showed that evacuation rates for herring fed *Artemia* were more rapid at higher prey densities, and because live and undigested prey were defecated, assimilation must have been low at these high prey densities.

Northern anchovy larvae, like herring, are con-

tinuous feeders, and at the high prey concentration, high consumption rates reduced the gut residence time and decreased digestion (assimilation; Tables 10, 11). At the lower prey concentration, the slower digestion time and increase in assimilation was not sufficient to compensate for the reduced consumption, and daily increase in weight, 15%, was less than the weight increase on the high-density diet, 21%. This result is similar to that in the recent study on assimilation by Pacific herring larvae fed *Brachionus* and *Artemia* (Boehlert and Yoklavich 1984). Using radioisotope tracers, Boehlert and Yoklavich found decreased assimilation at high food densities, but overall the larvae had a greater total energy gain at the high food densities because the higher food consumption more than compensated for the decreased assimilation.

Assimilation estimates, given here for northern anchovy larvae, fed two rotifer diets, averaged 53 and 79% and are somewhat higher than rates of 39-68%, depending on prey density, given by Boehlert and Yoklavich (1984) for Pacific herring. The assimilation estimates for northern anchovy larvae may not be reliable because the estimate assumes that weight-specific metabolic rates of fish fed both diets were equal. In addition, I made no attempt to correct for activity or to partition the portion of food assimilated into parts lost as feces and urine. Buckley and Dillman (1982) developed a technique to measure nitrogenous wastes of larval flounder. Assimilation efficiencies of 65-75% are commonly used in calculations of larval fish growth efficiencies (Ware 1975).

Estimates of gross growth efficiencies are not compromised by the above concerns. Larval northern anchovy gross-growth efficiencies increased with age, indicating that an increasing fraction of the calories consumed was translated into growth (Tables 10, 11). It is unrealistic that growth efficiencies would continue to increase. Brett and Groves (1979) suggested that for older fish growth rates become asymptotic with time. Growth efficiencies given here (24-46%) are consistent with growth efficiencies reported for other larval fish species (14-41% in Theilacker and Dorsey 1980) fed 1,000 or more prey per liter; reported efficiencies are high and extremely variable.

Direct observations of larval stomach contents showed that some rotifer-fed larvae fed at three times the average rate (C_{max}; Fig. 2). These fish may be the successful ones that survive in the field. Their high feeding rates would yield faster growth through the vulnerable larval stage. Feeding intensity also was highly variable for larvae eating copepods (Fig. 6), but the average number of copepods eaten was less than the average number of rotifers eaten (Table 2).

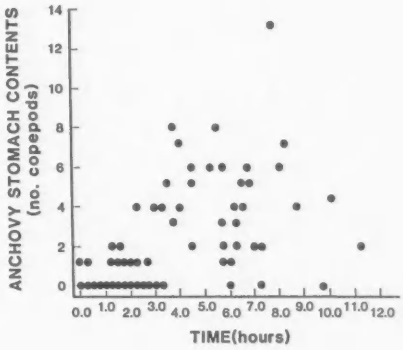

FIGURE 6.—Number of copepod nauplii observed in stomachs of 4.0-5.0 mm northern anchovy fed 2 copepods/mL. Each point is one larva.

Northern anchovy raised on copepods ate mainly *Gymnodinium*, augmenting their diet with copepod nauplii (Table 12). The stomachs of 96% of the 5-d-old larvae were full with *Gymnodinium* cells (Table 6). Fish were obtaining 60-90% of their daily caloric intake from *Gymnodinium*. This is evident by comparing the daily caloric intake (F_c) for day 5-6 larvae of equal size or weight that were fed copepods (Table 12) with those fed rotifers (Tables 10, 11). Consumption of 2-4 cells/minute can account for this energy input (4.2×10^{-5} cal/*Gymnodinium* cell [Vlymen 1977]), and successful feeding acts of this magnitude have been directly observed by Hunter (1981). Lasker and Zweifel (1978) developed a model (a modified version of Vlymen's [1977] model) to describe survival at sea in areas of various concentrations and proportions of large and small prey and concluded that large prey made very little contribution to survival of first-feeding larvae when sufficient (40 mL) small prey were available. As observed here, the ingestion of 10-20 copepod nauplii/day in addition to small *Gymnodinium* cells resulted in a growth rate of 0.35 mm/day, which is comparable to a rate of 0.37 mm/day reported for wild northern anchovy of similar age (Methot and Kramer 1979), and lends additional credence to Lasker and Zweifel's (1978) hypothesis that survival of northern anchovy depends on patchy (layered) distributions of small, abundant prey like *Gymnodinium*.

For all diets, an equivalent number of small prey,

TABLE 12.—Estimate of caloric input from copepods eaten by northern anchovy.

Diet	Age (d)	Standard length (mm)	Dry weight (μg)	Gut clearance rate (μg/h)	Gut contents Daily mean (μg)		Consumption Copepods (μg)	Consumption Body weight (%/d)	Consumption Copepods (cal/d)
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
	A	*l*	*W*	*r*	$\bar{c}$ est	$\bar{c}$ obs	F_w	$F_{w/W}$	F_c
Copepods	5	4.34	20.35	0.07	0.19	0.16	1.07	05	0.0052
2/mL	6	4.66	24.99	0.10	0.28	0.30	1.55	06	0.0076
and	7	4.99	30.43	0.15	0.41	0.43	2.26	07	0.0111
Gymnodinium	8	5.36	37.39	0.23	0.62	0.68	3.44	09	0.0169
	9	5.75	45.77	0.35	0.96	1.08	5.32	12	0.0261

[1]Hatching = Day 0.
[2]$l_t = 3.06\ e^{0.07t}$.
[3]$W = 0.297\ l^{2.88}$.
[4]$r = \bar{c}$ est/2.73 h (see text).
[5]Estimated using equation in Table 3.
[6]Average stomach contents calculated for t = >3 h; includes empty stomachs.
[7]$F_w = 12\ r + \bar{c}$ est.
[8]% body weight eaten/d as copepods.
[9]Calories/d, copepods; $F_w \times 4.9$ cal/mg (Table 1).

Gymnodinium cells, was available and the concentration of large prey was varied. Availability of large prey of a suitable size in the copepod diet was 10 times the number available in the low-density rotifer diet. Because 4 mm (day 5) larvae fed copepods ate mainly *Gymnodinium*, and those fed the low-density rotifer diet ate mainly rotifers (Tables 2, 6), copepods nauplii must be more difficult to catch than rotifers, and consequently larvae consumed the more abundant *Gymnodinium* cells. Larvae which consume prey as they are encountered, rather than choosing a diet that maximizes the energy gained per unit foraging time, have been labelled "number maximizers" as opposed to "energy maximizer" in the parlance of Griffiths (1975) and Hughes (1979). Additional evidence that points to northern anchovy feeding as "number maximizers" is that, when prey of the proper size were available, their feeding rates paralleled prey abundance (Tables 10, 11).

The energy budget I calculated for northern anchovy fed rotifers at two concentrations gives information on their growth requirements that can be translated to growth requirements in the field. My data support Boehlert and Yoklavich's (1984) and Checkley's (1984) conclusions that larval fish may exhibit a high growth rate or a high growth efficiency, but not both at the same time. Boehlert and Yoklavich studied Pacific herring, which are 2-4 times the weight of northern anchovy, but like anchovy feed continuously, and found that as consumption increased, the total amount of food assimilated continued to increase despite a decrease in the efficiency of the assimilation. Checkley studied Atlantic herring and found that the gross growth efficiencies of Atlantic herring increased with increasing consumption, but he showed that the relation was peaked, and by incorporating results from the literature for other species, he also described a decrease in growth efficiency at high consumption for larval fishes.

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LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.

BEYER, J. E.
1980. Feeding success of clupeoid fish larvae and stochastic thinking. Dana 1:65-91.

BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20:2-223.

BOEHLERT, G. W., AND M. M. YOKLAVICH.
1984. Carbon assimilation as a function of ingestion rate in larval Pacific herring, *Clupea harengus pallasi*. J. Exp. Mar. Biol. Ecol. 79:251-262.

BRETT, J. R., AND T. D. D. GROVES.
1979. Physiological energetics. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 8, p. 279-352. Acad. Press, N.Y. and Lond.

BUCKLEY, L. J., AND D. W. DILLMANN.
1982. Nitrogen utilization of larval summer flounder, *Paralichthys dentatus* (Linnaeus). J. Exp. Mar. Ecol. 59:243-256.

CHECKLEY, D. M., JR.
1984. Relation of growth to ingestion for larvae of Atlantic herring, *Clupea harengus* and other fish. Mar. Ecol. Prog. Ser. 18:215-224.

CHITTY, N.
1981. Behavioural observation of feeding larvae of bay anchovy *Anchoa mitchilli* and big eye anchovy *Anchoa lamprotaenia*. *In* R. Lasker and K. Sherman (editors), The early life history of fish, p. 320-321. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:320-321.

ELDRIDGE, M. B., J. A. WHIPPLE, AND M. J. BOWERS.
1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. Fish. Bull., U.S. 80:461-474.

ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.

GRIFFITHS, D.
1975. Prey availability and food of predators. Ecology 56: 1209-1214.

HAEGLER, C. W., AND B. N. OUTRAM.
1978. The effects of diet and ration on the growth and survival of Pacific herring, *Clupea harengus pallasi*, larvae. Fish. Mar. Serv. Tech. Rep. 767, 41 p.

HOUDE, E. D., AND R. C. SCHEKTER.
1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:441-453.
1983. Oxygen uptake and comparative energetics among eggs and larvae of three subtropical marine fishes. Mar. Biol. 72:283-293.

HUGHES, R. N.
1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. Am. Nat. 113: 209-221.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
1977. Behavior and survival of northern anchovy, *Engraulis mordax*, larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 19: 138-146.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae, p. 34-77. Univ. Wash. Press, Seattle and London.

HUNTER, J. R., AND R. LEONG.
1981. The spawning energetics of female northern anchovy *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

JOBLING, M.
1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish. Biol. 19:245-257.

KRAMER, D., AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5:345-353.

LASKER, R., AND J. ZWEIFEL.
1978. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. *In* John H. Steele (editor), Spatial pattern in plankton communities, p. 329-354. Plenum Publ. Corp.

LAURENCE, G. C.
1971. Digestion rate of larval largemouth bass. New York Fish Game J. 18(1):52-56.
1975. Laboratory growth and metabolism of the winter flounder *Pseudopleuronectes americanus* from hatching through metamorphosis at three temperatures. Mar. Biol. 32:223-229.
1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, *Pseudopleuronectes americanus*, larvae during the period from hatching to metamorphosis. Fish. Bull., U.S. 75:529-545.
1979. Larval length-weight relations for seven species of northwest Atlantic fishes reared in the laboratory. Fish. Bull., U.S. 76:890-895.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

LOVEGROVE, T.
1966. The determination of the dry weight of plankton and the various factors on the values obtained. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 429-467. Hafner Publ. Co., N.Y.

METHOT, R. D., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

MOFFATT, N. M.
1981. Survival and growth of northern anchovy larvae on low zooplankton densities as affected by the presence of a *Chlorella* bloom. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:475-480.

MOKSNESS, E.
1982. Food uptake, growth and survival of capelin larvae (*Mallorus villosus muller*) in an outdoor constructed basin. Fiskeridir. Skr. Ser. Havunders. 17:267-285.

O'CONNELL, C. P., AND PEDRO A. PALOMA.
1981. Histochemical indications of liver glycogen in samples of emaciated and robust larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:806-812.

O'CONNELL, C. P., AND L. P. RAYMOND.
1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

PEARCY, W. G., G. H. THEILACKER, AND R. LASKER.
1969. Oxygen consumption of *Euphausia pacifica*: The lack of a diel rhythm or light-dark effect, with comparison of experimental techniques. Limnol. Oceanogr. 14:219-223.

STAUFFER, G. D.
1973. A growth model for salmonids reared in hatchery environments. Ph.D. Thesis, Univ. Washington, Seattle.

THEILACKER, G. H., AND K. DORSEY.
1980. Larval fish diversity. *In* Workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 105-142. Intergov. Oceanogr. Comm. Rep. No. 28. UNESCO, Paris.

THEILACKER, G. H., AND A. S. KIMBALL.
1984. Comparative quality of rotifers and copepods as foods for larval fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 15:80-86.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer, *Brachionus plicatilis*, and its evaluation as a food for larval anchovies. Mar. Biol. 10:183-188.

VLYMEN, W.
1977. A mathematical model of the relationship between larval anchovy (*E. mordax*), growth, prey microdistribution and larval behavior. Environ. Biol. Fishes 2:211-233.

WARE, D. M.
1975. Relation between egg size, growth and natural mortality of larval fish. J. Fish. Res. Board Can. 32:2503-2512.

WERNER, R. G., AND J. H. S. BLAXTER.
1980. Growth and survival of larval herring (*Clupea harengus*) in relation to prey density. Can. J. Fish. Aquat. Sci. 37: 1063-1069.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

THIRTY-FOUR SPECIES OF CALIFORNIA ROCKFISHES: MATURITY AND SEASONALITY OF REPRODUCTION

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ABSTRACT

The viviparous rockfishes (*Sebastes* spp.) differ among species in age and size at maturity, and in the timing of peak spermatogenesis, fertilization, and larval extrusion. Age at 50% maturity ranges from 2 years in *S. jordani* to 9 years in *S. diploproa*. Within species, males usually mature either at the same age and size as females or at a younger age and smaller size. Rockfishes have two major seasons of larval extrusion, winter (November-March) or spring (April-July). The reproductive season for a particular species will fall within one of the major seasons throughout its geographic range. Within the major season, annual variations in the peak month of larval extrusion was observed for individual species. A long reproductive season and variations in the annual timing of that season are evidence of plasticity in the reproductive biology of rockfishes.

Reproductive development at the cellular level was compared with the coincident changes in the gross morphology of the gonads. The resulting description of the developmental sequences of the testes and ovaries enables the determination of maturity stage in the field.

Reproductive parameters such as age and size at maturity have been shown to be adaptive characteristics and are responsive to external pressures. For example, reduced population size due to fishing pressure may be associated with increased growth rate, reduced age at maturity, decreased fecundity, or a change in the gonadal index (Adams 1980; Gunderson 1980). For haddock, *Melanogrammus aeglefinis*, age at maturity was reduced and growth rates increased as the fishery increased (Templeman and Bishop 1979; Beacham 1983). Clupeoids shifted spawning location or time, and reduced age at maturity (Murphy 1977; Blaxter and Hunter 1982). A study of depleted populations of Pacific mackerel, *Scomber japonicus*, suggested a direct relationship between population size and age at maturity (Parrish and MacCall 1978). Pacific halibut, *Hippoglossus stenolepis*, stocks also showed reduced age at maturity and increased growth rates with reduced populations (Schmitt and Skud 1978). Age at maturity may thus be a useful indicator of heavy fishing mortality.

Rockfishes exhibit a variety of life history patterns, but only a few species have been studied in detail (Chen 1971; Miller and Geibel 1973; Patten 1973; Moulton 1977; Larson 1980; Love and Westphal 1981; McClure 1982). Previously, the most comprehensive work on the maturity of rockfishes was by Phillips (1964) and Westrheim (1975). Phillips (1964) sampled market landings from northern and central California over several years. For each of the 10 species he investigated, maturity was reported for the sexes combined, and ages at maturity were derived from back-calculated von Bertalanffy growth curves. Westrheim (1975) summarized 10 years of data gathered on trawl-caught fish off British Columbia and the Gulf of Alaska, for which he reported on size at maturity and reproductive seasonality. Most of the fish in his study are commercially important species for British Columbia and, except for three species, do not occur off California.

There are some difficulties in assessing maturity stages and reproductive seasonality in rockfishes. One problem is the use of external morphology of gonads to determine maturity stages. Some researchers have questioned the accuracy with which immature fish can be distinguished from resting, mature fish during the nonreproductive months (Gunderson et al. 1980; Rosenthal et al. 1982). Also, the potential reproductive season may be protracted and the peak time of reproduction may shift within this season, so that short-term studies may be misleading. Thus, reported variation in length and age at maturity between studies could be the result of uncertainty in maturity-stage determinations.

In this study, I clarify the determination of sexual maturity stages, determine age and size at sexual maturity, and survey the reproductive seasonality for 34 species of rockfishes from the waters off

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northern and central California, from Port San Luis to Crescent City. I outline the reproductive patterns among species and annual variation within species.

MATERIALS AND METHODS

Data for this study were collected between July 1977 and July 1982 from three sources: 1) a coastwide survey for adult rockfish made in July and August 1977 (Gunderson and Lenarz 1980); 2) an ongoing cooperative program, initiated in 1977 by the California Department of Fish and Game and the National Marine Fisheries Service, to sample the commercial (Sen 1984) and sport rockfish landings in northern and central California; and 3) a 1980 expansion of the cooperative program, to include data on gonad condition, prey items, seasonal fluctuation of interstitial fat, and gonad volumes. Additional collections were taken during cooperative survey trips with the National Marine Fisheries Service, Southwest Fisheries Center, and the California Department of Fish and Game. Fish were collected to supplement rarely sampled species and subadults that were not well represented in the three surveys.

Information on maturity was gathered primarily for seven species of commercial and sportfishing importance. Data for 27 additional species are presented, but these were inadequately sampled for statistical treatment of the data (Table 1). For each fish sampled from 1977 to 1982 the species, sex, and total length (mm) was determined in the field and otoliths were collected for age determination. The viscera from each of the 16,444 fish sampled from 1980 to 1982 were removed, preserved in 10% buffered formalin, and sent to the laboratory for analysis. In the laboratory the sex was verified and the maturity stage of the gonads was determined based on the criteria defined in this paper. Total length was measured from the most anterior part of the jaw to the dorsal tip of the caudal fin. When necessary, total lengths were converted to fork length to compare this study with others (Echeverria and Lenarz 1984).

Ages were determined for all fish investigated in this study. Most estimates of age were made from the surface of whole otoliths immersed in 70% ethyl alcohol, under a dissecting microscope at 12×. Standard techniques for counting annuli on whole otoliths were followed (Kimura et al. 1979; Shaw and Archibald 1981). Certain species such as *S. diploproa* required thin sectioning techniques for counting annuli (Beamish 1979). In some species it is difficult to determine what constitutes an annulus (Table 1), and consequently those ages have not been validated. The "break-and-burn" method of age determination (Chilton and Beamish 1982) is useful and more accurate than surface ages when aging fish older than 16 years (Tagart 1984). Ages were not redetermined in this study because the age at maturity occurs before 16 years. Maximum ages, however, may be underestimated.

The gonad conditions described for males are immature, maturing, mature (peak spermatogenesis), spent, and resting. For females, they are immature, maturing, mature (fertilized), ripe (eyed larvae), recently spent, and resting (Lyubimova 1965; Westrheim 1975; Gunderson et al. 1980). Histological sections were examined to define seasonal maturation and the sections were analyzed based on the criteria established by Moser (1967b) for *S. paucispinis* and by Lisovenko (1970) on *S. alutus* for mature fish. The development of germ cells into spermatozoa or mature oocytes was examined to determine the developmental sequence leading to maturity. Cellular development was compared with the external morphology (Westrheim 1975; Gunderson et al. 1980) to understand clearly the developmental sequence and to aid in the interpretation of maturity stages in the field. Gonads were subsampled from fish in all maturity stages. Whole gonads were sectioned and stained with hematoxylin. Histological sections were examined from 519 testes and 708 ovaries from 30 species (Table 1). Egg diameters were routinely measured from histological sections and checked against whole eggs using an ocular micrometer.

To determine age and size at maturity and reproductive seasonality, the approximate age and size when 50% and 100% of the males and females were mature were estimated for each species. For those commercial species for which large samples were available, I checked the accuracy of the rough maturity estimates by applying the method of Gunderson et al. (1980). These authors used the logistic model

$$P_x = \frac{1}{1 + e^{ax+b}}$$

where P_x = proportion mature at size x, and a and b are constants, to estimate the length at 50% maturity for a sample. I applied a transformation of this equation

$$\ln \frac{1}{P_x} - 1 = ax + b$$

to obtain estimates of a and b for size and age by

TABLE 1.—Sample characteristics used to determine age and size at maturity and seasonality for *Sebastes* from central California.

Species of *Sebastes* (common name)	Sampled		Total number		Histology	
	Age (yr)	Size (cm TL)	Immature (*N*)	Mature (*N*)	Males (*N*)	Females (*N*)
alutus (Pacific ocean perch)	5-16	26-54	2	83	2	2
auriculatus (brown rockfish)	1-19	10-52	140	281	16	20
aurora (aurora rockfish)	5-19	20-39	2	92	—	1
babcocki (redbanded rockfish)	3-24	23-66	23	137	1	2
carnatus (gopher rockfish)[1]	2-14	9-37	14	99	3	3
caurinus (copper rockfish)	3-20	19-57	49	276	17	14
chlorostictus (greenspotted rockfish)[2]	3-33	16-57	83	236	17	18
chrysomelas (black and yellow rockfish)[1]	1-12	9-38	19	159	—	—
constellatus (starry rockfish)[2]	2-15	12-44	58	152	6	4
crameri (darkblotched rockfish)	2-24	12-56	42	365	6	27
diploproa (splitnose rockfish)	3-27	13-40	44	266	1	3
elongatus (greenstriped rockfish)	2-21	13-31	33	215	16	12
entomelas (widow rockfish)[3]	3-31	26-58	182	2,285	25	28
flavidus (yellowtail rockfish)[3]	4-32	25-56	548	1,762	30	40
goodei (chilipepper)[3]	2-21	21-59	256	2,312	35	34
helvomaculatus (rosethorn rockfish)[1,2]	5-11	20-28	7	25	1	1
hopkinsi (squarespot rockfish)[1]	2-13	12-30	15	45	—	—
jordani (shortbelly rockfish)[1]	1-12	12-20	47	635	9	9
levis (cowcod)[1,2]	2-22	24-90	17	24	—	—
maliger (quillback rockfish)[1]	6-15	22-44	4	45	3	—
melanops (black rockfish)[3]	2-21	25-61	265	469	29	46
melanostomus (blackgill rockfish)	6-27	25-56	17	109	1	2
miniatus (vermilion rockfish)	5-30	30-67	12	96	7	2
mystinus (blue rockfish)[3]	2-23	21-49	263	1,297	16	48
nebulosus (china rockfish)[1]	1-17	8-44	13	56	4	3
ovalis (speckled rockfish)[1,2]	3-15	23-49	6	101	—	2
paucispinis (bocaccio rockfish)[3]	2-26	32-83	1,402	2,404	170	245
pinniger (canary rockfish)[3]	3-26	22-69	564	641	61	105
rosaceus (rosy rockfish)[2]	3-12	14-32	26	167	30	17
ruberrimus (yelloweye rockfish)[2]	3-30	25-69	46	86	8	6
rubrivinctus (flag rockfish)[1]	4-18	19-45	4	38	3	—
rufus (bank rockfish)[2]	2-24	19-54	25	137	—	—
saxicola (stripetail rockfish)	2-17	14-38	11	102	—	5
serranoides (olive rockfish)[1]	4-19	23-54	47	187	3	9

[1]Denotes species not sampled every month for determination of seasonality.
[2]Denotes difficult to interpret otoliths for age determination.
[3]Denotes species of major importance in the sport or commercial fisheries of California.

standard linear regression. These estimates of a and b were then used to calculate estimates of size or age (x) at 50% maturity ($P = 0.5$). This was done for all species with a sample of 10 specimens or more for each length or age. Where adequate data existed, P_{50} for a species was calculated by year and area to investigate possible yearly or geographic variation.

Reproductive stages for mature individuals were summarized by month, and the percentages of individuals at each reproductive stage were used to determine principal months of spermatogenesis (approximates mating), fertilization, and larval extrusion for each species. Seasonality was described only approximately for those species that were not present in all months sampled (Table 1).

Reproductive months for mature females were determined and the percentage containing eyed larvae was noted. Data from 1981 through 1985 were tabulated to compare annual variability in the

reproductive months and/or the principal month of parturition.

RESULTS

Moser (1967b) described the seasonal changes in gonads of mature *S. paucispinis* and should be consulted for details of morphology. In this study a general description of all maturity stages is included with emphasis on the immature gonad and the transitional stages, which are difficult to interpret. The transitional stages are 1) the determination of the first reproductive year, particularly in species with small maximum size; 2) the prespawned testis during spermatogenesis compared with the spawning and postspawned testis when spermatogenesis is completed and mating is in progress or just completed; 3) the unfertilized egg stage compared with the recently fertilized egg; and 4) the nonreproductive season, compared with the beginning of vitellogenesis or spermatogenesis when the gonads are beginning to mature. A comparison of external morphology with the histological sections indicates that the same sequence of spermatogenesis/vitellogenesis, mating, ovulation, fertilization, and larval extrusion is followed for each species in this study. There were not sufficient samples of all 31 species to discern what developmental variations might exist on the cellular level (Table 1).

Developmental Sequence of Ovaries

The germ cells in ovaries are clustered in oogonial nests, which are present throughout the year in varying numbers. The ovary of an immature rockfish (Gonad Stage 1) consists primarily of oogonial nests with oocytes <0.14 mm in diameter. The ovarian wall is translucent and thin (approximately 0.1 mm thick). Externally the ovary appears translucent with a tiny egg mass (Table 2).

Approaching the first year of maturity (Gonad Stage 2), the ovary is filled with oogonial nests, follicles begin to form around maturing oocytes, and the ovarian wall is translucent and thin. There is no evidence of the resorption and reorganization seen in spent ovaries. Externally the ovary appears pink through the thin wall, and eggs about 0.2 mm in diameter are visible.

As the reproductive season approaches (Gonad Stage 3) eggs are produced by the oogonial nests and vitellogenesis begins, resulting in eggs enlarging from 0.2 to 0.5 mm in diameter. Follicles form around the maturing eggs, a capillary network develops throughout the ovary, and the ovarian wall begins to thicken from 0.3 to 0.5 mm. Externally the ovary appears either white or yellow and firmly packed with eggs in grapelike clusters. The eggs expand during this stage, so that during maturation

TABLE 2.—Reproductive development at the cellular and external morphology level for ovaries of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Oogonial nests with oocytes <0.14 mm. Ovarian wall (OW) 0.1 mm thick.	Small and translucent to pink. Ovarian wall (OW) thin.
2. First year maturity	Oocytes <0.2 mm. No evidence of resorption.	Pink with visible eggs. No black pigmentation. OW thin.
3. Vitellogenesis	Mature oocytes 0.2-0.5 mm in diameter within follicles. OW 0.3-0.4 mm thick.	Yellow or white opaque eggs in grapelike clusters. OW thickening.
4. Fertilization	Oocytes 0.9 mm. Yolk globule disintegration, ovulation, fertilization.	Large clear eggs free in ovarian cavity, but enveloped by a network of capillaries.
5. Eyed larvae (parturition)	Larvae developed within chorion with eyes pigmented black or yellow.	Large, soft, gray. Ovary breaks easily, and is filled with eggs and fluid.
6. Spawned	Oocytes 0.08-0.64 mm in diameter. Resorption of blood vessels, atretic oocytes, and residual larvae. Collapsed egg cases. OW 0.5-1.0 mm thick.	Flaccid, reddish-purple, or grayish from residual larvae. OW thick and tough.
7. Resting	Resorption and reorganization. Proliferation of oogonial nests. OW 0.5-0.9 mm thick.	Firm, gray to pink. Tiny black dots indicate residual larvae, OW thick, tough, and loose from eggs.

the ovary swells in size. The eggs remain opaque, and held within a follicle.

Fertilized eggs (Gonad Stage 4) are about 0.9 mm in diameter and have shed their follicles, and the yolk globules have disintegrated. Externally the eggs appear translucent yellow or white and are no longer held in tight grapelike clusters. They are held within an elaborate capillary network, not totally free within the ovary, though they are no longer held within a follicle.

Development of the embryos continues for about a month (Moser 1967a) until they develop pigmented eyes (Gonad Stage 5) and become ready for release. The pigmented eyes are usually black except in *S. ruberrimus* where they are yellow. Externally the ovary is gray (from the pigmented eyes) and very fragile. It breaks easily when handled and usually some larvae are prematurely extruded when the adult is captured.

After normal release of the larvae (Gonad Stage 6), the ovary consists primarily of an elaborate vascular system, larvae that were not extruded, and a few eggs which failed to develop (atretic oocytes). Externally it appears very mushy and reddish gray, with an opaque and flaccid ovarian wall.

Resorption and reorganization of the ovary (Gonad Stage 7) occur until vitellogenesis begins (Gonad Stage 3) again. During the months of reorganization (Figs. 1-7) there is evidence of residual larvae, eggs, and capillaries being resorbed, and a proliferation of oogonial nests producing eggs for the next reproductive season. The ovarian wall is between 0.5 and 0.9 mm thick. Externally the ovary is compact and loosely encased by an opaque wall. During resorption the ovary changes from reddish brown to grayish brown. When vitellogenesis begins again (Gonad Stage 3) the ovary appears yellow or white. There are usually a few pigmented eyes being resorbed through Gonad Stage 3 from the previous year's brood.

The principal external characteristic of an immature ovary entering the first reproductive season is the wall, which is thin (0.1 mm) and translucent. There are also no residual pigmented eyes in the ovary. A spent and maturing ovary from a mature fish usually contains remnants of resorbed larvae (evidenced as black dots) encased by a thick, opaque ovarian wall (0.5 to 0.9 mm).

Developmental Sequence for Testes

It is often difficult to distinguish an immature from a resting testis in rockfish because the presence of sperm in the testis is not necessarily an indication of the fish's maturity. Understanding the developmental sequence of spermatogenesis can help to identify the reproductive stage any time of year (Table 3).

Histological examination shows that the immature testis (Gonad Stage 1) consists of germ cells, primary spermatogonia, and secondary spermatogonia which lend a whitish color at the periphery. Externally the testis is threadlike and translucent, often with a hint of white from the developing spermatogonia.

Spermatogenesis begins at the periphery of the testis and moves centripetally, filling the lumen, the efferent ducts, and finally the sperm duct. A male approaching the first year of maturity (Gonad Stage

TABLE 3.—Reproductive development at the cellular and external morphology level for testes of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Germ cells, primary and secondary spermatogonia.	Small, threadlike; transparent to white at periphery.
2. First year maturity	Spermatozoan cysts throughout testis. No residual sperm in tubules or ducts.	Small, ribbonlike, and white. No evidence of sperm in central duct (translucent).
3. Spermatogenesis	Large spermatozoan cysts throughout testis with spermatozoa in lumen.	Milky white and swollen, sperm throughout testis in cross section.
4. Spawning	Sperm duct and lumen filled with spermatozoa. Spermatogenesis ceases at periphery.	Large, soft, white; sperm flows freely when cut. Center of testis white, periphery becoming translucent.
6. Recently spawned	Abundance of germ cells at periphery. Resorption of sperm by tubular boundary cells.	Center is white in cross section, with the periphery becoming firm and darker.
7. Resting	Reorganization of testis. Germ cells line spermatogenic tubules.	Firm, compact, and vaguely triangular. Color dark gray/brown.

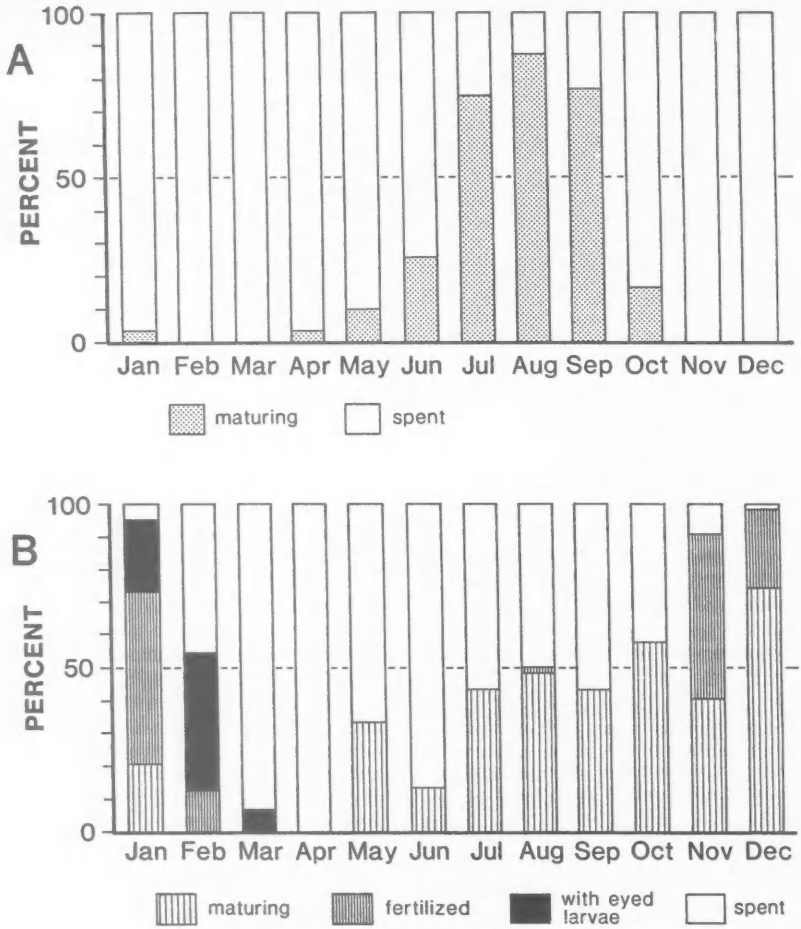

FIGURE 1.—A. Reproductive seasonality of mature males of *Sebastes entomelas* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. entomelas* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

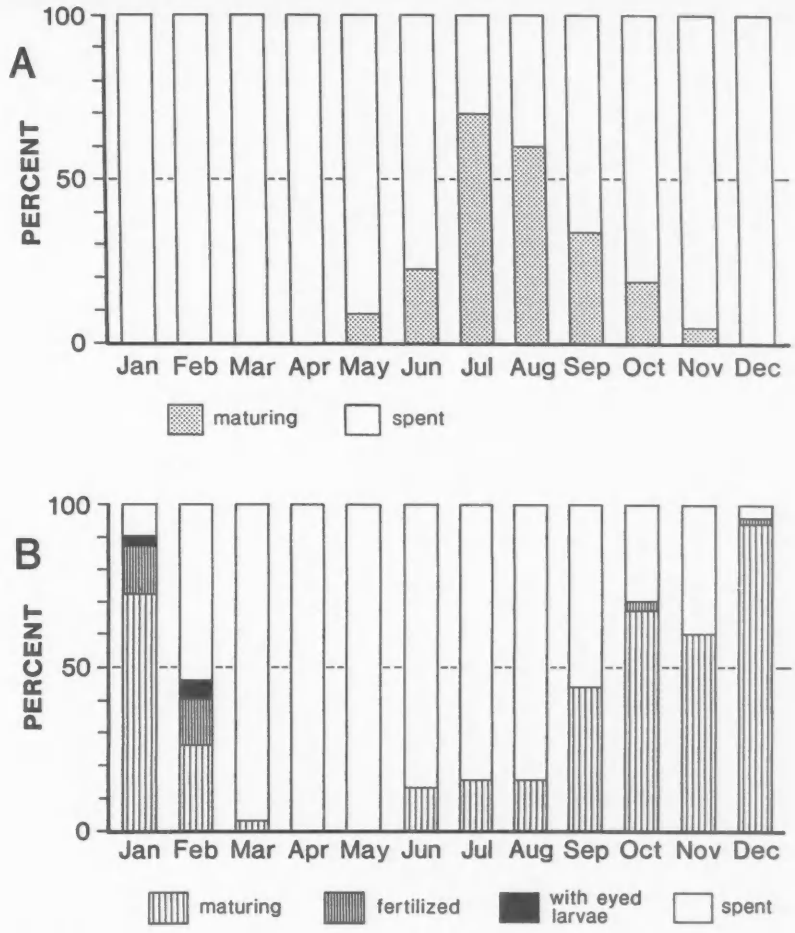

FIGURE 2.—A. Reproductive seasonality of mature males of *Sebastes flavidus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. flavidus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

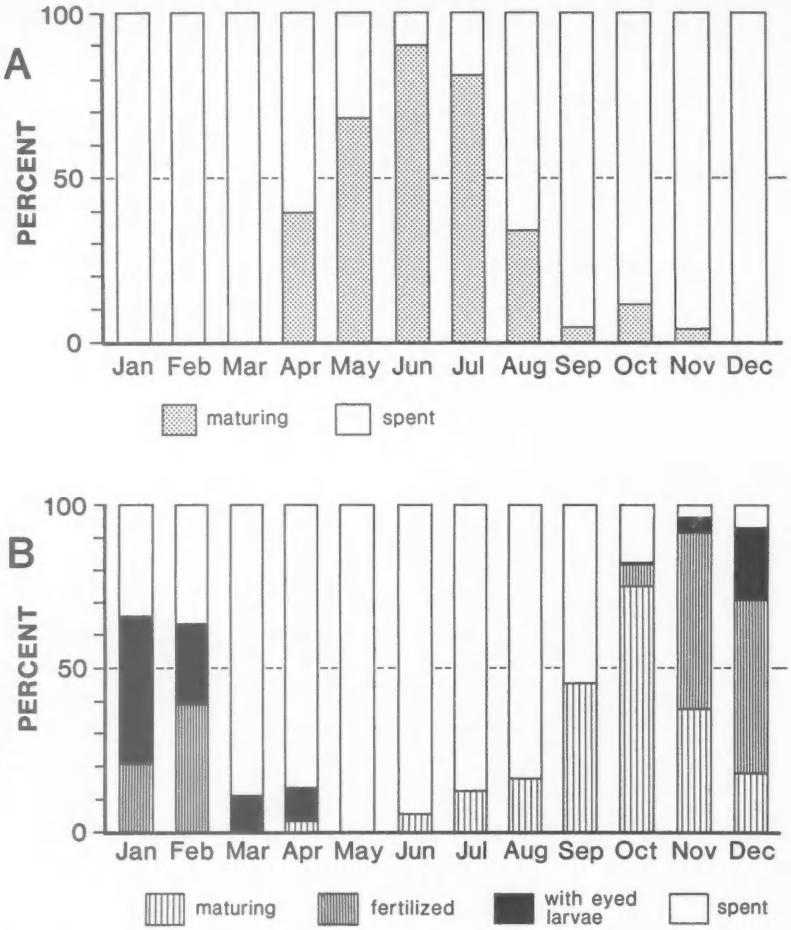

FIGURE 3.—A. Reproductive seasonality of mature males of *Sebastes goodei* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. goodei* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

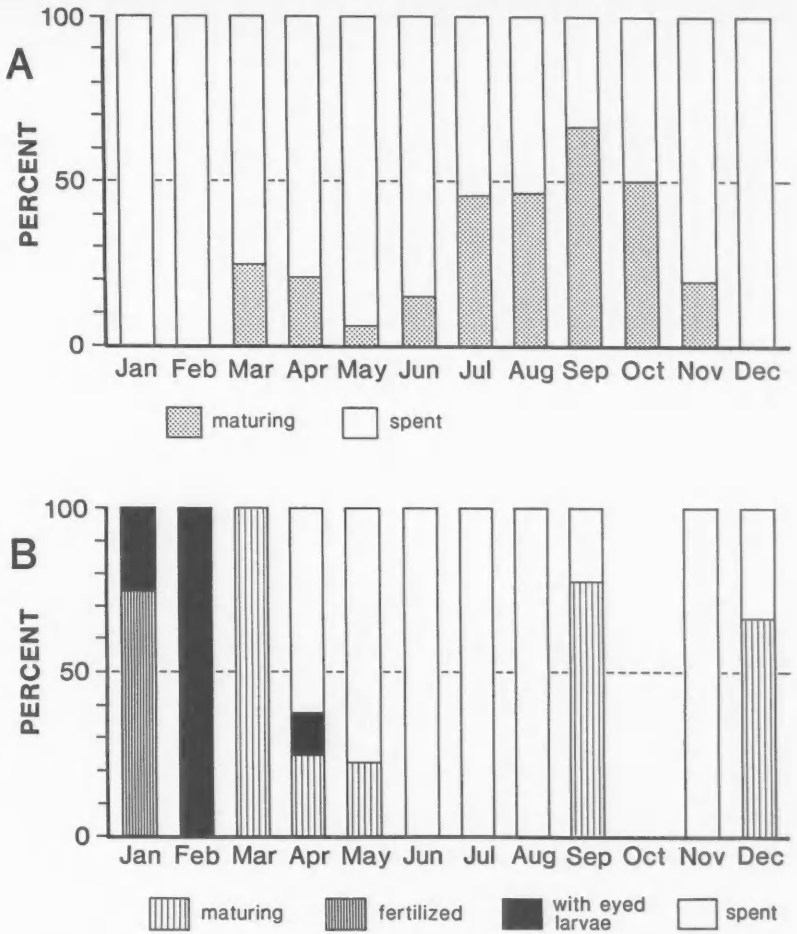

FIGURE 4.—A. Reproductive seasonality of mature males of *Sebastes melanops* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. melanops* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

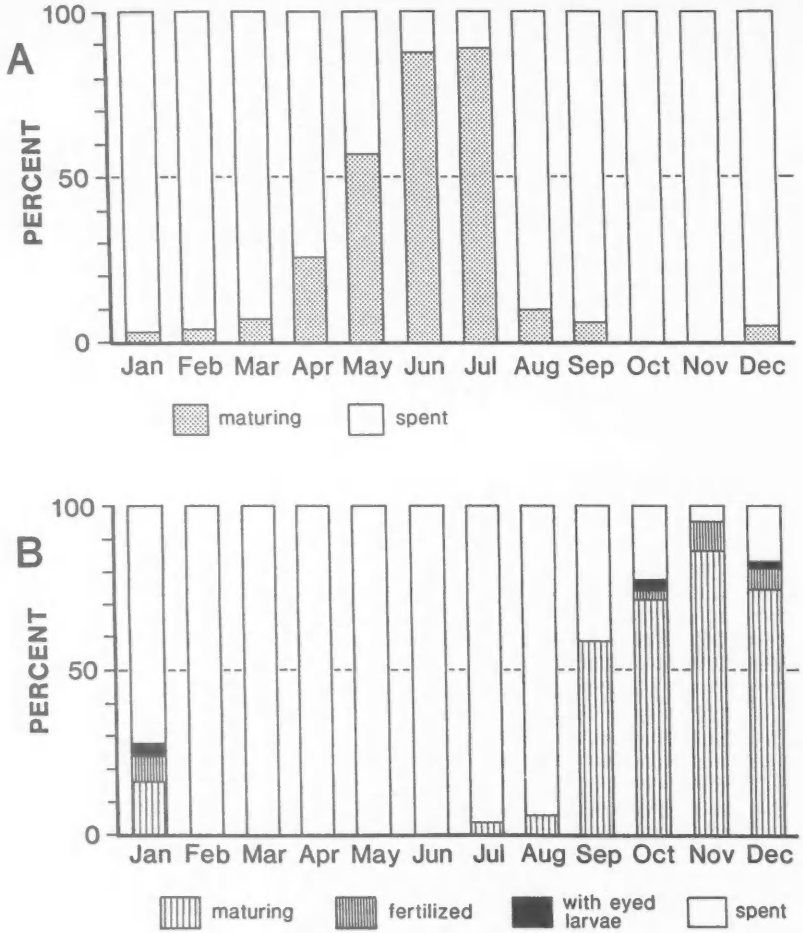

FIGURE 5.—A. Reproductive seasonality of mature males of *Sebastes mystinus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. mystinus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

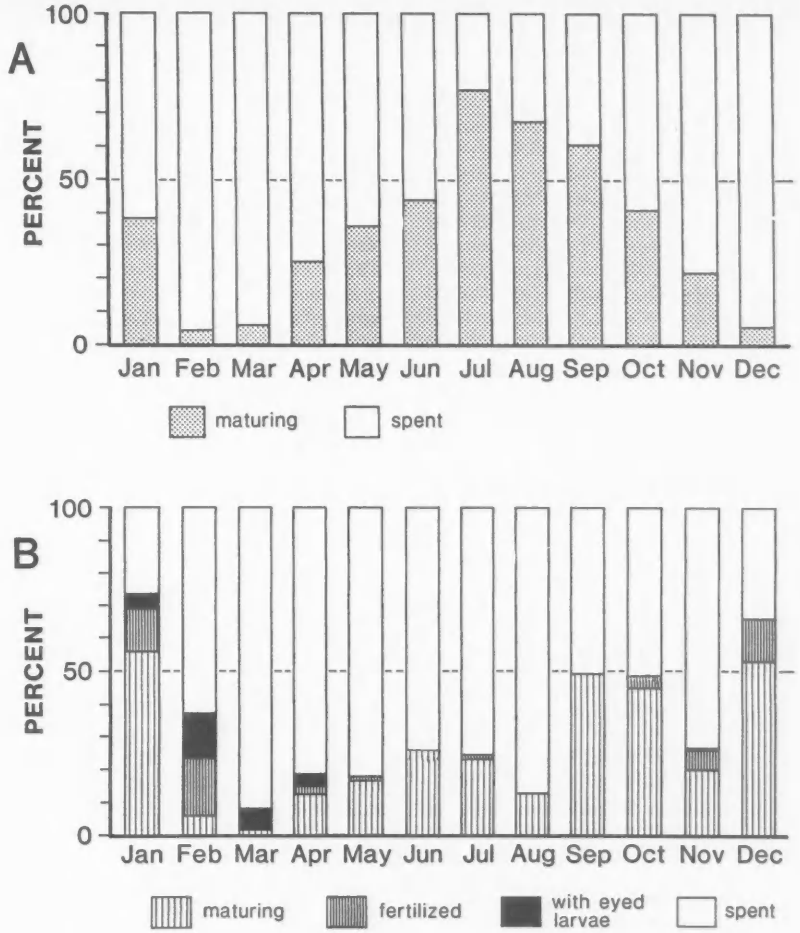

FIGURE 6.—A. Reproductive seasonality of mature males of *Sebastes paucispinis* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. paucipinis* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

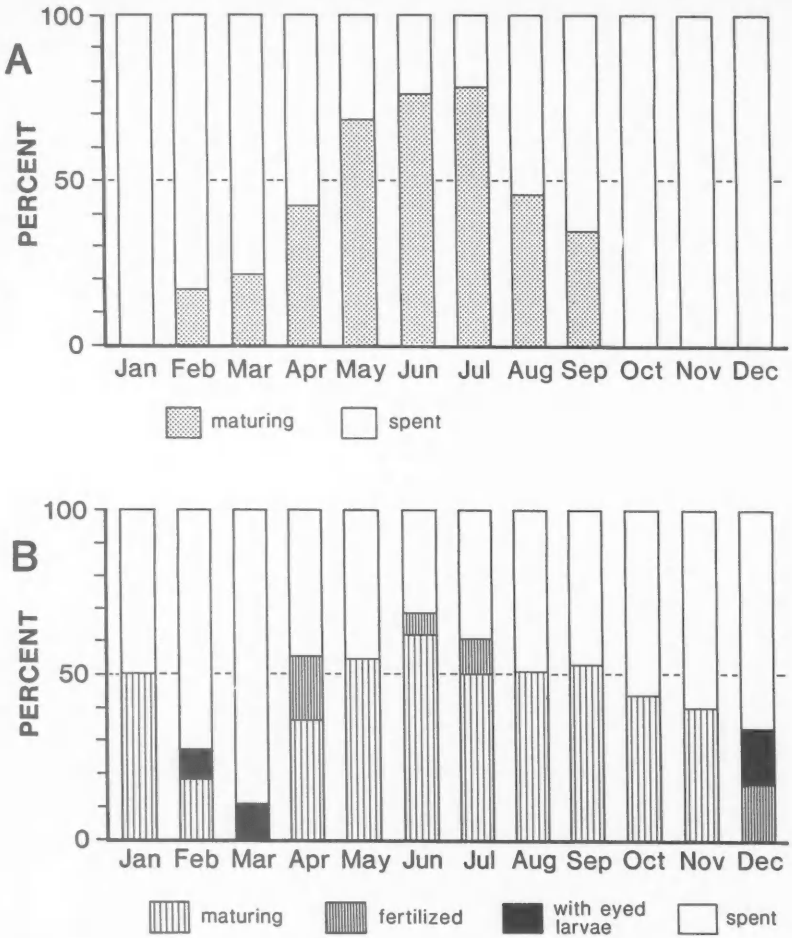

FIGURE 7.—A. Reproductive seasonality of mature males of *Sebastes pinniger* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. pinniger* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

2) has spermatogonial cysts developing throughout the testis. There is no sign of spermatozoa in the sperm duct. Externally, the testes appear slightly swollen and white; in cross section they are translucent in the center because of the absence of sperm in the sperm duct.

In a maturing male (Gonad Stage 3) spermatozoa appear throughout the testis in spermatozoan cysts. The sperm duct often contains remnants of residual sperm from the previous reproductive season. In a cross section the testis is swollen and whitish at the periphery and brownish off-white in the center because of the presence of residual sperm in the sperm duct.

As the reproductive season approaches (Gonad Stage 4) the spermatozoan cysts burst open, releasing spermatozoa into the efferent ducts and the sperm duct. Externally the testis is large, soft, and very white, sperm flows freely when the testis is pressed or cut. During the reproductive season spermatogenesis has ceased and the spermatozoa have moved from the periphery towards the sperm duct so that the periphery becomes hard and discolored. The central area may be swollen with sperm.

At the end of the reproductive season (Gonad Stage 7), the testis undergoes resorption and reorganization, wherein smooth muscle cells, connective tissue, and scattered residual spermatozoa, constituting cellular detritus, are evident in the histological sections. At the periphery, a new generation of germ cells reorganizes along the spermatogenic tubules. Externally the testis is a compact, irregular triangular shape that appears gray or brown.

An understanding of the developmental sequence on the cellular level aids in the interpretation of gonad stage in the field. The four, difficult to interpret, transitional stages can be clarified: 1) The first reproductive year is indicated by a white periphery (sperm) and an absence of sperm in the center of a cross section of testis, a thin ovarian wall and no residual pigmented eyes in ovaries. 2) The center of the prespawned testis is firm and a dark cream color (residual sperm); the periphery is white and swollen with sperm. The postspawned testis usually shows signs of white fluid (sperm) in the sperm duct and is firm and a dark cream color at the periphery. 3) Unfertilized eggs are opaque yellow or white held tightly in grapelike clusters while fertilized eggs are a translucent yellow or white and the outer eggs can be separated from each other. 4) Vitellogenesis is indicated by a deep yellow color and swelling of the eggs so that the ovarian wall fits tightly around the eggs; spermatogenesis is indicated by a softening and swelling of the testis and a whitening at the periphery.

Reproductive Maturity and Seasonality

Maturity was observed over a broad age and size range within species throughout the years sampled. The age and size at first maturity, 50% maturity and 100% maturity were estimated for males and females of each species (Table 4). Males reached 50% maturity either at the same or younger age than females. Size at 50% maturity is generally similar or somewhat smaller for males than for females of the same species. The standard linear regressions were run on the transformed logistic for the seven principal species occurring in this study, resulting in similar estimates of age at 50% maturity for *S. entomelas*, *S. flavidus*, *S. goodei*, *S. melanops*, *S. mystinus*, *S. paucispinis*, and *S. pinniger* (Table 5), and similar, if not exact, sizes at 50% maturity as estimates derived from the raw data. Maturity for species without sufficient data for statistical treatment are estimated from the raw data.

The reproductive season in *Sebastes* can be long with larval extrusion (parturition) seen in females of some species for up to 9 months (Table 6). From all the data collected between 1977 and 1984 a summary of principal month of spermatogenesis, fertilization, and parturition was determined for 32 species (Table 7). A span of 1 to 5 months between peak spermatogenesis and fertilization is seen. The time, when males ripen and mate, is not dependent upon the eggs being fully mature. The time between fertilization and parturition is usually about 1 month (Moser 1967a).

Reproductive seasonality for the principal species sampled is displayed graphically in Figures 1-7. Seasonality histograms are available, upon request, for most species investigated. The general trend in the seasonality of *Sebastes* is a prolonged reproductive period for each maturity stage. This trend is seen in the seven most abundant species sampled (Figs. 1-7). Spermatogenesis (Gonad Stage 3) occurs over 3 to 5 months before the testes are fully ripe (Gonad Stage 4). The timing of mating is estimated from the appearance of testes swollen with sperm. At least part of the male population is ready for mating for a period of 2 to 4 months. In females, generally, fertilized eggs (Gonad Stage 4) are found 1 to 3 months after mating. Eyed larvae (Gonad Stage 5) appear from 1 to 4 months after fertilized eggs were observed and were present in the sampled population for 3 to 6 months, usually with a

TABLE 4.—Estimated age and size at 1st, 50% and 100% maturity for given in cm

Species of *Sebastes*	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
alutus	—	—	5	28	7	32	7	26	7	26	7	32
auriculatus	3	26	5	31	10	38	3	26	5	31	10	38
aurora	5	28	—	—	5	28	5	28	—	—	5	28
babcocki	3	27	4	31	5	36	3	32	4	34	6	41
carnatus	4	17	4	17	5	21	4	17	4	17	5	21
caurinus	3	30	4	32	7	40	5	31	6	34	8	41
chlorostictus	4	25	6	27	12	38	5	26	6	28	9	34
chrysomelas	3	14	3	16	5	20	3	14	3	15	5	19
constellatus	6	28	7	30	12	36	5	23	6	27	9	34
crameri	3	25	4	27	7	36	3	24	4	27	6	34
diploproa	7	20	9	22	10	29	6	18	7	19	9	23
elongatus	7	23	7	23	10	27	5	18	7	23	10	27
entomelas[1]	3	31	5	36	8	41	3	29	5	37	8	40
flavidus[1]	4	30	6	35	11	43	4	27	7	36	11	42
goodei[1]	2	26	3	31	7	38	2	29	3	34	6	39
helvomaculatus	7	22	7	22	10	27	5	20	8	23	10	27
hopkinsi	4	15	5	16	5	17	5	17	5	18	7	21

[1]Denotes samples from 1980-82 study only.

peak month of larval extrusion. The external appearance of individual ovaries indicates that larvae are in the eyed stage and ready for release throughout the ovary.

The total number of mature females observed during the reproductive months, and the percentage containing eyed larvae is presented for three commercially important species (Figs. 8-10). For the years 1981-85, variations in the months of parturition and/or the peak month is seen. *Sebastes entomelas* (Fig. 8) showed an annual variation in the months of parturition but not in the peak months (January-February). The peak month for *S. goodei* (Fig. 9) varied from December to February, and in *S. paucispinis* (Fig. 10) from December to March. A variation in which months larval extrusion occurs is seen in all three species. Chi-square tests showed the percentages to be dependent upon year and month. Therefore, there is a relationship between the percent-number of mature females with eyed larvae seen in a particular month, and reproductive year.

DISCUSSION

The reproductive biology of *Sebastes* follows the sequence of spermatogenesis, vitellogenesis, mating, ovulation, fertilization, and larval extrusion (Moser 1967b). As in other viviparous fishes (Turner 1947), sperm can apparently survive within the ovary for many months. In *S. mentella*, ovulation and the activation of sperm coincide with a change in pH (Sorokin 1967). The histological evaluation of the gonads in *Sebastes* of northern California confirms that spermatogenesis is generally completed and mating occurs before the completion of vitellogenesis. The length of time males are fully ripe can be up to 2 months in various species, and the delay between the time males are fully ripe and fertilization (sometimes up to 4 months) indicates that mating does not coincide with fully mature ova (Figs. 1-7). Testes are observed in decreasing degrees of ripeness after spermatogenesis has ceased. This indicates that one mating does not void the testes; males may mate more than once per season. Ovulation in teleosts is regulated by steroids and prostaglandins, which in turn are influenced to some degree by temperature, pheromones, or spatial/temporal cues (Stacey 1984). The presence of sperm in the ovaries of *Sebastes* does not trigger final oocyte maturation and ovulation; therefore, ovulation is probably influenced by environmental conditions. Thus knowing which conditions influence ovulation is necessary to determine some of the factors contributing to a successful reproductive year, as measured by the percent mature females with eyed larvae.

The costs of reproduction for females include the development of a highly vascular network throughout the ovaries, the nourishing of developing embryos (Boehlert and Yoklavich 1984), and the metabolism of waste products from the embryos (Moser 1967a). The ovaries must accommodate the added gonadal weight and volume until larval extrusion.

Sebastes from northern and central California collected 1977-82. Lengths total length (TL).

Species of *Sebastes*	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
jordani	1	12	2	14	5	20	2	12	3	14	4	19
levis	4	32	4	32	4	32	4	32	4	32	5	37
maliger	4	22	4	22	7	31	6	26	6	26	7	28
melanops[1]	3	25	6	36	10	43	5	30	7	41	11	48
melanostomus	6	29	7	33	10	39	7	30	8	35	9	36
miniatus	5	35	5	38	8	43	5	37	5	37	9	46
mystinus[1]	4	22	5	27	9	32	5	22	6	29	11	35
nebulosus	3	26	4	27	6	30	3	26	4	27	6	30
ovalis	4	28	4	28	5	30	4	28	4	28	5	29
paucispinis[1]	3	32	3	42	7	55	3	36	4	48	8	60
pinniger[1]	4	28	7	40	9	45	4	27	9	44	13	54
rosaceus	4	16	6	20	8	25	4	15	6	20	8	25
ruberrimus	6	36	7	40	8	46	6	36	7	40	8	46
rubrivinctus	5	29	5	30	6	32	5	29	8	34	10	38
rufus	—	27	3	31	4	36	2	32	3	34	4	41
saxicola	3	15	3	16	4	17	2	17	2	17	3	18
serranoides	4	32	5	33	8	38	4	32	5	35	8	39

TABLE 5.—Standard linear regression used to estimate age (yr) and size (cm) at 50% maturity for males (M) and females (F) in seven species of *Sebastes*. Slope and *y*-intercept were estimated from the equation $\ln \frac{1}{P_x} - 1 = ax + b$. r = correlation coefficient, N = number of ages or sizes used in the regressions; each N represents at least 10 observations per age or size.

Species of *Sebastes*	Sex	Variable	*y*-intercept	Slope	50% maturity	*r*	*N*
entomelas	M	age	4.5598	−1.0006	5	−0.9588	6
		size	10.1042	−0.3162	33	−0.7649	11
	F	age	5.4800	−0.7982	5	−0.9647	5
		size	28.4810	−0.7810	37	−0.9667	4
flavidus	M	age	2.9748	−0.4994	6	−0.9577	10
		size	13.7834	−0.3964	35	−0.9718	14
	F	age	5.3731	−0.7757	7	−0.9541	9
		size	15.7482	−0.4331	36	−0.9723	13
goodei	M	age	1.1620	−0.4093	3	−0.9263	9
		size	7.7618	−0.3044	31	−0.8730	10
	F	age	3.7624	−1.1129	3	−0.9775	6
		size	12.2400	−0.3740	34	−0.9650	15
melanops	M	age	4.3841	−0.8011	6	−0.9769	6
		size	13.7147	−0.3814	36	−0.9411	6
	F	age	5.0627	−0.7149	7	−0.9760	8
		size	11.0749	−0.2720	41	−0.9520	16
mystinus	M	age	1.3482	−0.3669	5	−0.8530	10
		size	4.3885	−0.2049	27	−0.6778	11
	F	age	5.0097	−0.8022	6	−0.9680	9
		size	9.5090	−0.3368	29	−0.9218	17
paucispinis	M	age	1.7138	−0.6677	3	−0.9431	8
		size	10.7040	−0.2564	42	−0.9196	16
	F	age	3.5175	−0.8232	4	−0.9232	7
		size	13.7028	−0.2876	48	−0.9565	20
pinniger	M	age	3.7804	−0.5845	7	−0.9710	9
		size	11.2047	−0.2837	40	−0.9500	16
	F	age	5.1221	−0.5897	9	−0.9800	11
		size	11.5621	−0.5897	44	−0.9460	15

TABLE 6.—Months of parturition for species of *Sebastes* that occur in the northeastern Pacific Ocean. All available data are listed by area (results of this study in parentheses).

Species of *Sebastes*	Gulf of Alaska	British Columbia	Washington	Oregon	North-Central California	Southern California
aleutianus		Apr.[1]		May[2]		
alutus	May[3], Apr.-May[1]	Mar.[3]	Mar.[4]	Jan.-Apr.[2]	(Jan.-Mar.)	
auriculatus				June[5], May[6]	(Dec.-Jan.; May-July), May[7]	
aurora		>June[1]			(Mar.-May)	
babcocki		Apr.[1]		Apr.[2]	(May)	
borealis		Apr.[1]				
brevispinis		>May[1]				
carnatus					(Mar.-May), May[7]	
caurinus			Mar.[8], Apr.[6,9,5]		(Feb.)	
chlorostictus				Apr.[2]	(Apr.-Sept.)	Apr.-July[10], July[11]
chrysomelas					(Feb.-Mar.), Jan.-May[7]	
constellatus					(Apr.-May)	Mar. + May[10,11]
crameri	<June[1]	Feb.[1]		Feb.-Mar.[2]	(Nov.-Mar.), Nov.-Mar.[7]	
diploproa		July[1]	July[6]	Apr.-May[12]	(Jan.-Sept.), Feb.-July[13]	
elongatus		>June[1]		Apr.-May[12]	(May-July)	
ensifer						Feb. + May[10]
entomelas		Apr.[1]		Jan.[2,14]	(Dec.-Apr.), Nov.-Mar.[13]	
eos						Apr.-June[11]
flavidus		Mar.[1]	Jan.-Apr.[4]	Jan.-Mar.[2]	(Jan.-July), Nov.-Mar.[13]	
goodei					(Nov.-June), Nov.-Mar.[13]	Oct.-Mar.[11]
helvomaculatus	>May[1]	>May[1]			(May-June)	
hopkinsi					(Feb.-Mar.)	
jordani				Feb.[2]	(Feb.-Apr.), Nov.-Mar.[13]	
lentiginosus						Mar.[10]
levis					(Dec.-Feb.)	Dec.-Jan.[11]
maliger	May-July[15]	Apr.[1,16], May[5]			(Apr.-July)	
melanops		Jan.[17], <Apr.[1]		Jan.[17]	(Jan.-May)	
melanostomus					(Feb.-Apr.)	
miniatus					(Sept.) Nov.[11], Nov.-Mar.[13]	Nov.[11]
mystinus					(Nov.-Jan.), Nov.-Jan.[18], Jan.-Mar.[19]	
nebulosus					(Jan.-June), Jan.[20]	
nigrocinctus		May[1]				
ovalis					(May)	Jan.-May[11]
paucispinis		<Feb.[1]	Jan.-Apr.[4]	Jan.-Feb.[2]	(Jan.-May), Nov.-Mar.[11]	Oct.-Mar.[11]
pinniger		>Feb.[1]		Dec.-Apr.[2]	(Dec.-Mar.), Nov.-Mar.[11]	
proriger				Apr.-July[2]	(July-Aug.)	
reedi		May[1]		Feb.-May[15]		
rosaceus					(Apr.-July)	Mar. + May[10,11]
ruberrimus	June-Aug.[15]	May[1]	July[6]	Mar.-Apr.[2], Apr.-May[12]	(Apr.-June)	
rubrivinctus		May[1]		Apr.-May[12]	(July)	Mar.-June[10]
rufus					(Dec.-May)	
saxicola		Feb.[1]		Feb.[2]	(Jan.-Mar.), Nov.-Mar.[13]	
serranoides					(Jan.-Mar.)	Jan.[16]
simulator						Feb.-Mar.[10]
umbrosus						Apr.[10]
wilsoni		June[1]				
zacentrus	>May[1]	July[1]		Mar.-July[2], Apr.-May[12]	(May-June)	

[1]Westrheim 1975.
[2]W. H. Barss, Oregon Department of Fish and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. 1985.
[3]Lyubimova 1965.
[4]Gunderson et al. 1980.
[5]Washington et al. 1978.
[6]DeLacy et al. 1964.
[7]Larson 1980.
[8]Patten 1973.
[9]Moulton 1977.
[10]Chen 1971.
[11]Moser 1967a.
[12]Hitz 1962.
[13]Phillips 1964.
[14]Barss and Echeverria 1987.
[15]Rosenthal et al. 1981.
[16]Love and Westphal 1981.
[17]Dunn and Hitz 1969.
[18]Wales 1952.
[19]Miller and Geibel 1973.
[20]Burge and Schultz 1973.

TABLE 7.—Reproductive seasonality for *Sebastes* from central California collected 1977-84. Listed by taxonomic order (Barsukov 1981).

Species of *Sebastes*	Principal month(s) of spermatogenesis	fertilization	parturition
melanostomus	Nov.	Feb.	Feb.
aurora	Apr.	?	Apr.
ruberrimus	Dec.	Apr.	June
chrysomelas	?	Jan.	Feb.
carnatus	Dec.	?	Mar.
nebulosus	?	Jan.	Jan.
auriculatus	May	May	June
caurinus	Dec.	Jan.	Feb.
maliger	Dec.-Jan.	Apr.	Apr.
elongatus	?	Apr.	May
babcocki	Jan.	?	May
saxicola	?	Dec.	Jan.
diploproa	June	June	July
crameri	?	Dec.	Jan.
alutus	Sept.-Oct.	?	Mar.
pinniger	Oct.	Dec.	Dec.
miniatus	July	?	Sept.
levis	Sept.-Oct.	Oct.	Dec.
rosaceus	May	May	June
constellatus	Dec.	Feb.	Apr.
chlorostictus	Feb.	Apr.	May
goodei	Oct.	Dec.	Jan.
jordani	Nov.	Jan.	Feb.
paucispinis	Oct.	Dec.	Feb.
ovalis	Nov.	?	May
rufus	Nov.	Nov.	Feb.
hopkinsi	Dec.	Feb.	Mar.
entomelas	Oct.	Jan.	Feb.
mystinus	Aug.	Jan.	Jan.
melanops	Oct.	Jan.	Feb.
flavidus	Sept.	Jan.	Feb.
serranoides	Nov.	Jan.	Feb.

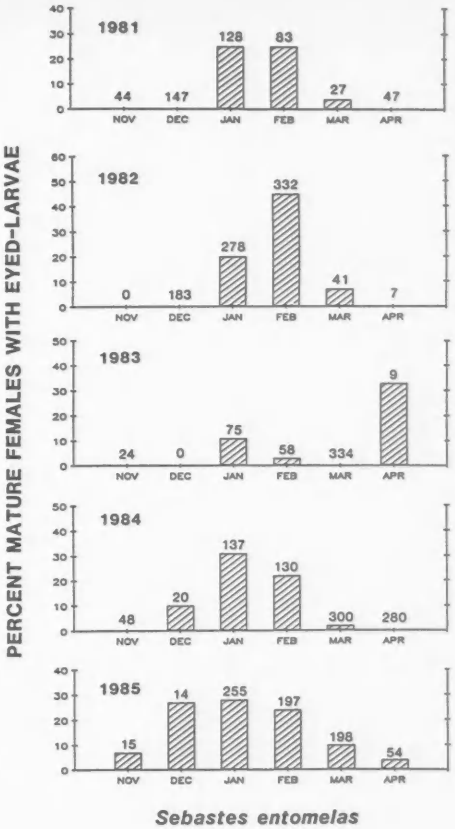

FIGURE 8.—Percent of mature female *Sebastes entomelas* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

Females are exposed to changing environmental factors from year to year, so flexibility in the timing of their greatest reproductive involvement may be advantageous. The apparent flexibility of the period between mating and larval extrusion may be a mechanism to optimize reproductive success. A long and variable period of larval extrusion is exhibited by the rockfish group (Figs. 8-10). The evidence of two spawnings per season have been reported for *S. paucispinis* (Moser 1967a), *S. ovalis*, and *S. constellatus* (MacGregor 1970). Multiple broods are indicated by the presence of eyed larvae undergoing resorption in the ovary concurrently with vitelloginic eggs at least 0.4 mm in diameter. During the years and throughout the area of this study, evidence of multiple broods was rare: only one *S. paucispinis* gonad showed evidence of a multiple brood. Moser's (1967b) detailed description of the histology of multiple broods indicates the development and extrusion of a second brood follows within 2 months of the first. In this study, two distinct seasons of larval extrusion, December and June, were noticed in *S. auriculatus* sampled from a limited area (Pt. Reyes-Half Moon Bay) (Table 6) in north-central California. The entire reproductive sequence in *Sebastes* seems to reflect a plasticity for reproduction that may enable the individual to respond adaptively to environmental factors.

The consequences of the reproductive biology in *Sebastes* include the absence of strong spawning pulses, the possibility of multiple mating of males, and flexibility in the timing of fertilization. Apparently mating is not restricted to a short period

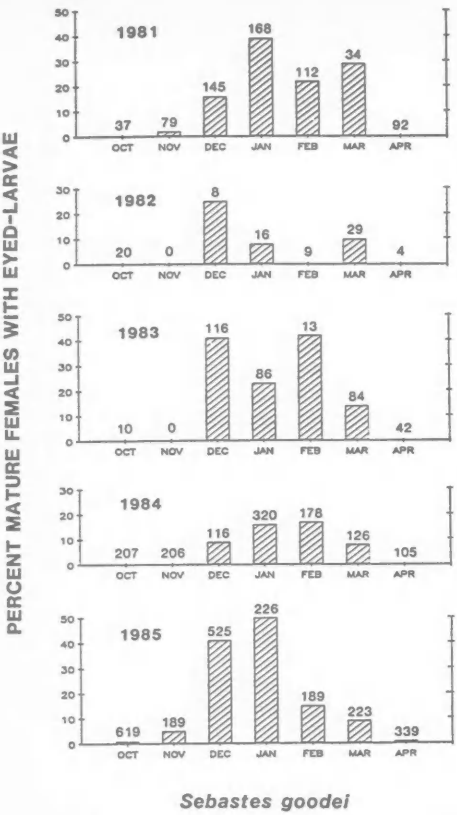
PERCENT MATURE FEMALES WITH EYED-LARVAE
1981
37 79 145 168 112 34 92
OCT NOV DEC JAN FEB MAR APR
1982
20 0 8 16 9 29 4
OCT NOV DEC JAN FEB MAR APR
1983
10 0 116 86 13 84 42
OCT NOV DEC JAN FEB MAR APR
1984
207 206 116 320 178 126 105
OCT NOV DEC JAN FEB MAR APR
1985
619 189 525 226 189 223 339
OCT NOV DEC JAN FEB MAR APR
Sebastes goodei

FIGURE 9.—Percent of mature female *Sebastes goodei* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

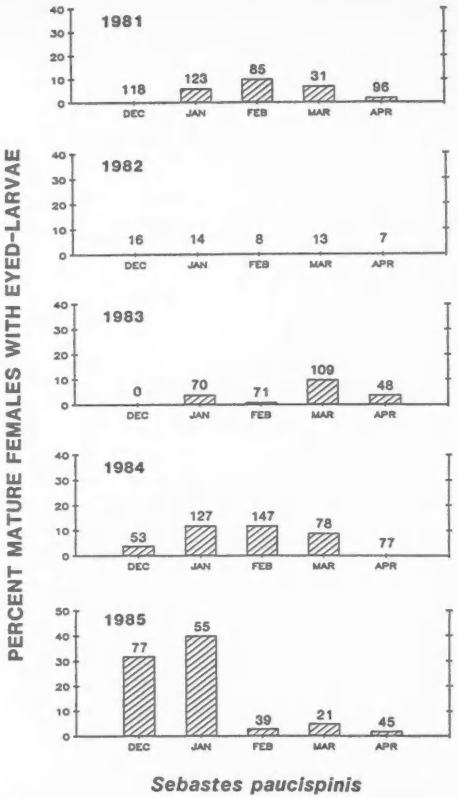

FIGURE 10.—Percent of mature female *Sebastes paucispinis* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

of time and elaborate displays to induce ovulation are not necessary. It is not surprising, therefore, to find so little information regarding mating behavior in the most speciose and populous group of fishes in north-central California (Helvey 1982).

Ages and sizes at maturity from this study generally agree with findings in the literature, but sometimes exhibit large discrepancies (Table 8). The variability has possible sources: differences in age determination techniques, length measurements, identification of the immature gonad stage, or sampling at times of the year when it is difficult to distinguish immature from resting fish. Previous studies on maturity often focused on adult populations or were based on samples taken only during summer, when most species are not in reproductive condition (Westrheim 1975; Gunderson et al. 1980; Rosenthal et al. 1981, 1982). The differentiation of an immature gonad stage versus mature "resting" gonads is most difficult and subject to error during the nonreproductive months.

Age and size at 50% maturity by area and year were calculated for *S. flavidus*, *S. goodei*, and *S. paucispinis* (Table 9). Age and size at maturity did not differ geographically but did vary between years. Age varies up to 1 year and size varies up to 3 cm. Apparently, there is some variability in age and size at maturity within a population between years. The normal range of variation of size and age

TABLE 8.—Age and size at 50% maturity for male (M) and female (F) *Sebastes* by area. All lengths are converted to fork length for comparison (Echeverria and Lenarz 1984).

Species of *Sebastes*	Alaska	British Columbia	Washington	Oregon	California	this study
auriculatus						
M			4 yr, 23 cm FL[1]			5 yr, 31 cm FL
F			4 yr, 25 cm FL			5 yr, 31 cm FL
entomelas						
M		37 cm FL[2]		4 yr, 33 cm FL[3]	4 yr, 29 cm FL[4]	5 yr, 32 cm FL
F		38 cm FL		7 yr, 38 cm FL		5 yr, 36 cm FL
flavidus						
M	11-15 yr[5]	40 cm FL, 40.5 cm FL[2,6]			5 yr, 31 cm FL[4]	6 yr, 32 cm FL
F	41-45 cm FL	42 cm FL, 45 cm FL				7 yr, 33 cm FL
goodei						
M				26 cm FL[6]	4 yr, 28 cm FL[4]	3 yr, 29 cm FL
F				37 cm FL	4 yr, 30 cm FL	3 yr, 32 cm FL
melanops						
M	10-13 yr, 40-42 cm FL[5]		3 yr, 21 cm FL[7]	5 yr[8]		6 yr, 35 cm FL
F	9-12 yr, 39-42 cm FL		3-4 yr, 33 cm FL	6 yr		7 yr, 40 cm FL
mystinus						
M				3 yr[8]	6-7 yr[9]	5 yr, 26 cm FL
F				4 yr	6 yr	6 yr, 28 cm FL
paucispinis						
M		<57 cm FL[2]	5 yr, 45 cmFL[7]		4 yr[4]	3 yr, 39 cm FL
F		<62 cm FL	6 yr, 48 cm FL		37 cm FL	4 yr, 45 cm FL
pinniger						
M		41 cm FL[2,6]		12 yr, 39 cm FL[8]	5-6 yr[4]	7 yr, 39 cm FL
F		48 cm FL		10 yr, 43 cm FL	33 cm FL	9 yr, 43 cm FL

[1]Washington et al. 1978; [2]Westrheim 1975; [3]Barss and Echeverria 1987; [4]Phillips 1964; [5]Rosenthal et al. 1982; [6]Gunderson et al. 1980; [7]Barker 1979; [8]McClure 1982; [9]Miller et al. 1967.

at maturity should be determined before subtle shifts in these parameters are studied.

Later spawning in high latitude populations occurs in some teleosts as a response to temperature and photoperiod (Wootton 1984). The existence of geographical trends for spawning months can be determined for a species if data exist for the same months and years. Parturition occurred somewhat earlier in the southern end of the range of *S. maliger*, *S. ruberrimus*, and *S. entomelas*. *Sebastes maliger* extruded larvae between May and July off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes ruberrimus* extruded larvae between June and August off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes entomelas* extruded larvae in February off Oregon and in January off California in 1982 (Barss and Echeverria 1987) (Table 6). For species where comparable data exist, parturition is earlier in the southern end of the species range.

TABLE 9.—Age and size of three *Sebastes* species at 50% maturity derived from linear regressions for males (M) and females (F) by area and by year for the area between Crescent City and Morro Bay.

		S. flavidus		*S. goodei*		*S. paucispinis*	
Data base	Sex	yr	cm TL	yr	cm TL	yr	cm TL
North of Point Arena	M	—	—	4	—	3	43
	F	—	—	4	—	4	48
South of Point Arena	M	—	—	4	31	3	43
	F	—	—	4	33	4	47
April 1980-March 1981	M	6	35	4	31	3	43
	F	7	37	4	34	4	48
April 1981-March 1982	M	7	38	5	33	3	42
	F	6	36	4	32	4	47
April 1980-Mach 1982	M	6	35	4	31	3	43
	F	7	36	4	34	4	48

Reproductive seasonality can be classified into one of two broad seasons, early (winter) or late (spring-summer) (Phillips 1964), which seems to hold true throughout a species range (Table 6). The duration of larval extrusion varies from 1 to 9 months and is species-specific. Closely related species have similar seasons of parturition, but the peak month may differ (Table 7).

Data on parturition may be useful when investigating recruitment by estimating annual reproductive success. To predict year-class strength for species of *Sebastes*, it must be possible to identify species in the juvenile stages. Juvenile identifications have been described for 18 species of rockfish

that occur off California (Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980, 1981; Anderson 1983); the difficulties of differentiating between similar species are evident in these studies. Knowledge of the principal month of parturition may be a useful tool when identifying species in the age 0 population. Principal month of parturition would have to be documented for the year that recruitment is investigated.

Life history parameters that are interrelated, such as growth, maturity, and fecundity, can be influenced by external conditions, such as temperature, prey abundance, and predation (Stearns and Crandall 1984). The manner in which they can be affected is species-specific and may change in a predictable manner. Observed changes that coincide with reduced population sizes include increase in growth rates (Templeman and Bishop 1979), decrease in age at maturity (Murphy 1977; Parrish and MacCall 1978; Schmitt and Skud 1978; Templeman and Bishop 1979), and decrease in size at maturity (Alm 1959; Pitt 1975). Stearns and Crandall (1984) proposed that changes in age and/or size at maturity are determined by genetic as well as environmental factors, so that populations will respond in a predictable manner. A shift in either the age or size at maturity in *Sebastes* may be an indication of a change in population densities. In order to detect any population changes, age and size at maturity for species should be determined yearly and within a well-defined geographic area. Fish of the estimated age and size at first maturity should be included—sampling from market fish tends to yield only mature fish. Ages should be determined from the same fish that are sampled for maturity.

Fecundity in poikilotherms is generally related to size; changes in growth rates and size at maturity will affect fecundity. Fecundity often relates more to body size in short-lived species and to available energy in long-lived species (Ware 1980). Fecundity increases with size in at least some species of *Sebastes* (Phillips 1964), but annual reproductive success may be linked to available energy. Gonad volumes of female *S. flavidus* were reported for 1981 (Guillemot et al. 1985) and compared with volumes measured during the El Niño winter of 1983-84 (Lenarz and Wyllie Echeverria 1986); this comparison showed reduced gonad volumes in *S. flavidus* for the 1983 reproductive season. Whether the decreased gonad volume was due to egg size or number was not determined.

Shifts in age and/or size at maturity may occur in species that have a multigenerational, late-maturing population. In his studies of flatfish populations, Roff (1982) predicted that size at maturity would be primarily influenced by size-dependent mortality and that changes in size at maturity would occur in species where growth to a minimal size is more adaptive than early reproduction. Changes in age at maturity will more likely occur in species that mature early. Changes in size, rather than age, at maturity would most likely occur in *Sebastes* subjected to overfishing or long-term environmental stress.

General changes in life history parameters may be predictable according to a species' position on the *r*-*K* selection continuum. Increased fishing mortality resulting in decreased populations may affect life history parameters by increasing growth rates, reducing age at first maturity, increasing fecundity at age (Adams 1980; Gunderson 1980), and reducing variability in the gene pool by reducing the number of spawning groups in the more *K*-selected species (Leaman and Beamish 1984). The reproductive strategy of *Sebastes* reflects more *K*-type characteristics, which include later maturity, slower growth rates, lower individual fecundity, or some degree of parental care (Garrod and Horwood 1984). The *K*-type reproductive strategy enables a species to minimize the effects of a poor reproductive year (Roff 1984). A disadvantage for a heavily fished *K*-type species is the late age at maturity, as exists in *Sebastes*, so that the advantage of many reproductive seasons must be balanced against adult population size to obtain an allowable harvest.

The reproductive strategy of *Sebastes*, with multiple generations reproducing simultaneously and the plasticity of annual timing, results in a buffered system. The populations of exploited stocks of *Sebastes* should be able to recover from a single year of high mortality due either to poor recruitment or to adult mortality. However, overfished populations or long periods of poor recruitment could result in a reduced size at maturity and a corresponding reduced fecundity.

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LITERATURE CITED

ADAMS, P. B.
1980. Life history patterns in marine fishes and their consequences for fisheries management. Fish. Bull., U.S. 78:1-12.

ALM, G.
1959. Connection between maturity, size and age in fishes. Inst. Freshwater Res. Drottningholm Rep. 40, 145 p.

ANDERSON, T. W.
1983. Identification and development of nearshore juvenile rockfishes (genus *Sebastes*) in central California kelp forests. M.A. Thesis, San Francisco State Univ., San Francisco, CA, 216 p.

BARKER, M. W.
1979. Population and fishery dynamics of recreationally exploited marine bottomfish of northern Puget Sound. Diss. Abstr. Int. B Sci. Eng. 40(6):2497.

BARSS, W. H., AND T. ECHEVERRIA.
1987. Marturity of widow rockfish (*Sebastes entomelas*) from the northeast Pacific 1977-1981. *In* W. H. Lenarz and D. R. Gunderson (editors), Proceedings of the Widow Rockfish Workshop, 11-12 December 1980, Tiburon, CA. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC 48:13-18.

BARSUKOV, V. V.
1981. A brief review of the subfamily Sebastinae. J. Ichthyol. 21:1-26.

BEACHAM, T. D.
1983. Variability in size and age at sexual maturity of haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf in the northwest Atlantic. Can. Tech. Rep. Fish. Aquat. Sci. 1168, 33 p.

BEAMISH, R. J.
1979. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can. 36:1395-1400.

BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20:1-223.

BOEHLERT, G. W., AND M. YOKLAVICH.
1984. Reproduction, embryonic energetics, and the maternal fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. (Woods Hole) 167:354-370.

BURGE, R. T., AND S. A. SCHULTZ.
1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Resour. Tech. Rep. 19, 433 p.

CHEN, L. C.
1971. Systematics, variation, distribution, and biology of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. 18, 115 p.

CHILTON, D. E., AND R. J. BEAMISH.
1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. 60, 102 p.

DELACY, A. C., C. R. HITZ, AND R. L. DRYFOOS.
1964. Maturation, gestation, and birth of rockfish (*Sebastodes*) from Washington and adjacent waters. Wash. Dep. Fish., Fish. Res. Pap. 2(3):51-67.

DUNN, J. R., AND C. R. HITZ.
1969. Oceanic occurrence of black rockfish (*Sebastes melanops*) in the central north Pacific. J. Fish. Res. Board Can. 26:3094-3097.

ECHEVERRIA, T., AND W. H. LENARZ.
1984. Conversions between total, fork, and standard lengths in 35 species of *Sebastes* from California. Fish. Bull., U.S. 82:249-251.

GARROD, D. J., AND J. W. HORWOOD.
1984. Reproductive strategies and the response to exploitation. *In* G. W. Potts and R. J. Wootton (editors), Fish reproduction: strategies and tactics, p. 367-384. Acad. Press, Lond.

GUILLEMOT, P. J., R. J. LARSON, AND W. H. LENARZ.
1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae; *Sebastes*). Fish. Bull., U.S. 83:299-311.

GUNDERSON, D. R.
1980. Using *r-K* selection theory to predict natural mortality. Can. J. Fish. Aquat. Sci. 37:2266-2271.

GUNDERSON, D. R., P. CALLAHAN, AND B. GOINEY.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74-79.

GUNDERSON, D. R., AND W. H. LENARZ.
1980. Cooperative survey of rockfish and whiting resources off California, Washington, and Oregon, 1977: Introduction. Mar. Fish. Rev. 42(3-4):1.

HELVEY, M.
1982. First observations of courtship behavior in rockfish, genus *Sebastes*. Copeia 1982:763-770.

HITZ, C. R.
1962. Seasons of birth of rockfish (*Sebastodes* spp.) in Oregon coastal waters. Trans. Am. Fish. Soc. 91:231-233.

KIMURA, D. K., R. R. MANDAPAT, AND S. L. OXFORD.
1979. Method, validity, and variability in the age determination of yellowtail rockfish, *Sebastes flavidus*, using otoliths. J. Fish. Res. Board Can. 36:377-383.

LAROCHE, W. A., AND S. L. RICHARDSON.
1980. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:901-924.
1981. Development of larvae and juveniles of the rockfishes *Sebastes entomelas* and *S. zacentrus* (family Scorpaenidae) and occurrence off Oregon, with notes on head spines, of *S. mystinus*, *S. flavidus*, and *S. melanops*. Fish. Bull., U.S. 79:231-257.

LARSON, R. J.
1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50:221-239.

LEAMAN, B. M., AND R. J. BEAMISH.
1984. Ecological and management implications of longevity in some northeastern Pacific groundfishes. Int. N. Pac. Fish. Comm. Bull. 42:85-97.

LENARZ, W. H., AND T. WYLLIE ECHEVERRIA.
1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. Fish. Bull., U.S. 84:743-745.

LISOVENKO, L. A.
1970. A study of spermatogenesis in Pacific rockfish *Sebastodes alutus* (Gilbert) from the Gulf of Alaska. *In* Moiseev, P. A. (editor), Soviet fisheries investigations in the northeastern Pacific, Part V, p. 248-266. Israel Program Sci. Transl. Jerusalem.

LOVE, M. S., AND W. V. WESTPHAL.
1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. Fish. Bull., U.S. 79:533-545.

LYUBIMOVA, T. G.
1965. Main stages in the life cycle of the rockfish *Sebastodes alutus* (Gilbert) in the Gulf of Alaska. Tr. VNIRO 49:85-111.

MACGREGOR, J. S.
1970. Fecundity, multiple spawning, and description of the gonads in *Sebastodes*. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 596, 12 p.

MCCLURE, R. E.
1982. Neretic reef fishes of central Oregon: aspects of life histories and the recreational fishery. M.S. Thesis, Oregon State Univ., Corvallis, OR, 94 p.

MILLER, D. J., M. W. ODEMAR, AND D. W. GOTSHALL.
1967. Life history and catch analysis of the blue rockfish (*Sebastodes mystinus*) off central California 1961-1965. Calif. Dep. Fish Game, MRO Ref. No. 67-14, 130 p.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

MOSER, H. G.
1967a. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773-797.
1967b. Seasonal histological changes in the gonads of *Sebastodes paucispinis* (Ayres), an ovoviviparous teleost (family Scorpaenidae). J. Morph. 123:329-351.

MOSER, H. G., AND E. H. AHLSTROM.
1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981-996.

MOULTON, L. L.
1977. An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. Thesis, Univ. Washington, Seattle, 181 p.

MURPHY, G. I.
1977. Clupeoids. *In* J. A. Gulland (editor), Fish population dynamics, Ch. 12, p. 283-308. John Wiley & Sons, Lond.

PARRISH, R. H., AND A. D. MACCALL.
1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish Game, Fish Bull. 167, 110 p.

PATTEN, C. G.
1973. Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102:412-416.

PHILLIPS, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

PITT, T. K.
1975. Changes in abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides platessoides*. J. Fish. Res. Board Can. 32:1383-1398.

RICHARDSON, S. L., AND W. A. LAROCHE.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family: Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1-46.

ROFF, D. A.
1982. Reproductive strategies in flatfish; a first synthesis. Can. J. Fish. Aquat. Sci. 39:1686-1698.
1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. 41:989-1000.

ROSENTHAL, R. J., L. J. FIELD, AND D. MYER.
1981. Survey of nearshore bottomfish in the outside waters of southeastern Alaska. Prepared for Alaska Dep. Fish Game, Comm. Fish. Div., Juneau, AK, 91 p.

ROSENTHAL, R. J., L. H. HALDORSON, L. J. FIELD, V. MORAN-O'CONNELL, M. G. LARIVIERA, J. UNDERWOOD, AND M. C. MURPHY.
1982. Inshore and shallow offshore bottomfish resources in the southeastern Gulf of Alaska (1981-1982). Prepared for Alaska Dep. Fish Game, Comm. Fish. Div., Juneau, AK, 166 p.

SCHMITT, C. C., AND B. E. SKUD.
1978. Relation of fecundity to long-term changes in growth, abundance and recruitment. Int. Pac. Halibut Comm. Sci. Rep. 66, 31 p.

SEN, A. R.
1984. Sampling commercial rockfish landings in California. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-45, 95 p.

SHAW, W., AND C. P. ARCHIBALD.
1981. Length and age data of rockfishes collected from B.C. coastal waters during 1977, 1978, and 1979. Can. Data Rep. Fish. Aquat. Sci. 289, 119 p.

SOROKIN, V. P.
1967. Some data on gametogenesis and sexual cycles of the Pacific Ocean Scorpaenidae. Tr. PINRO 20:304-315.

STACEY, N. E.
1984. Control of the timing of ovulation by exogenous and endogenous factors. *In* G. W. Potts and R. J. Wootton (editors), Fish reproduction: strategies and tactics, p. 207-222. Acad. Press, Lond.

STEARNS, S. C., AND R. E. CRANDALL.
1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. *In* G. W. Potts and R. J. Wootton (editors), Fish reproduction: strategies and tactics, p. 13-33. Acad. Press, Lond.

TAGART, J. V.
1984. Comparison of final ages assigned to a common set of Pacific ocean perch otoliths. Wash. Dep. Fish. Tech. Rep. 81, 36 p.

TEMPLEMAN, W., AND C. A. BISHOP.
1979. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of St. Pierre bank. ICNAF Res. Bull. 14:77-83.

TURNER, C. L.
1947. Viviparity in teleost fishes. Sci. Mon. 65:508-518.

WALES, J. H.
1952. Life history of the blue rockfish *Sebastodes mystinus*. Calif. Fish Game 38:485-498.

WARE, D. H.
1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37:1012-1024.

WASHINGTON, P. M., R. GOWAN, AND D. H. ITO.
1978. A biological report on eight species of rockfish *Sebastes* spp. from Puget Sound, Washington. Northwest Alaska Fisheries Center, 50 p. [Processed rep.]

WESTRHEIM, S. J.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

WOOTTON, R. J.
1984. Introduction: strategies and tactics in fish reproduction. *In* G. W. Potts and R. J. Wootton (editors), Fish reproduction: strategies and tactics, p. 1-12. Acad. Press, Lond.

DISTRIBUTION, ABUNDANCE, REPRODUCTION, FOOD HABITS, AGE, AND GROWTH OF ROUND SCAD, *DECAPTERUS PUNCTATUS*, IN THE SOUTH ATLANTIC BIGHT[1]

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ABSTRACT

Five years of bottom trawling indicated that round scad were abundant and widely distributed throughout the South Atlantic Bight in summer and fall, but less abundant and restricted to deeper (28-110 m), warmer (>15°C) waters in winter and spring. Adults and juveniles were spatially segregated, with adults dominating catches in inner and outer shelf regions and juveniles dominating midshelf regions year round. Catches over sponge-coral habitat were significantly greater than catches over sand bottom in winter, whereas catches over the two bottom types were similar in other seasons. This seasonal change in distribution may relate to higher productivity and temperature stability of live bottom habitats. Stomach contents indicated that round scad are diurnally feeding zooplanktivores; diets changed seasonally and increased in prey diversity with growth. Round scad spawn repeatedly from March through September. Daily growth analysis revealed that both sexes mature in 4-5 months at approximately 11 cm fork length. The life span of round scad could not be determined because the growth record of otoliths of most adults was irregular.

Fishes of the genus *Decapterus* occur in most neritic and some oceanic waters of tropical, subtropical, and temperate latitudes. Little is known of the biology of most species, except for those species which support fisheries in the Hawaiian Islands, the Philippines, Japan, and the west coast of Africa (Yamaguchi 1953; Tiews et al. 1970; Akaoka 1971; Boely et al. 1973). Although the taxonomy of Indo-Pacific species is unclear (Berry 1968), three species are recognized in the western North Atlantic: the redtail scad, *Decapterus tabl* Berry; the mackerel scad, *D. macarellus* (Cuvier); and the round scad, *D. punctatus* (Agassiz).

The round scad occurs in the western Atlantic from Nova Scotia to Rio de Janeiro, Brazil, and throughout the West Indies and Bermuda (Berry 1968); however, little information is available concerning its basic biology. The distribution of the species has been determined from purse seine catches in the Gulf of Mexico (Klima 1971), where it supports a bait fishery, and from bottom trawl catches over sand bottom habitat in the South Atlantic Bight (Wenner et al. 1979a, b, c, d, 1980). The location and duration of the spawning season has been ascertained from ichthyoplankton surveys in the eastern Gulf of Mexico (Aprieto 1974; Leak 1981). In addition, Leak (1981) determined larval mortality and production, and estimated biomass and potential yield of round scad in the eastern Gulf of Mexico. The objectives of this study were to provide information on seasonal distributions, relative abundance, reproduction, feeding habits, age, and growth of round scad in the South Atlantic Bight.

METHODS

Seasonal Distribution and Relative Abundance

A stratified random sampling design (Grosslein 1969) was used to assign trawling stations within six depth zones (9-18 m, 19-27 m, 28-55 m, 56-110 m, 111-183 m, 184-366 m) on nine seasonal cruises (Table 1). A total of 739 stations were completed on the continental shelf and upper continental slope between Cape Fear, NC and Cape Canaveral, FL. Fishes were captured in a 3/4 scale version of a "Yankee No. 36" otter trawl (Wilk and Silverman 1976) with a 11.9 m headrope, a 16.5 m footrope, and a 1.3 cm stretch mesh cod end liner. Although catches of pelagic fishes by bottom trawls seldom provide accurate estimates of absolute abundance of these species, they probably do reflect relative

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TABLE 1.—Catch statistics for *Decapterus punctatus* in the South Atlantic Bight. n = number of trawls; $\bar{x}_{st}$ = stratified mean catch tow^{-1}; $\bar{x}_{ln}$ = stratified mean catch tow^{-1} for $\ln(x + 1)$ transformed data; $\bar{x}_{Bliss}$ = Bliss (1967) estimate of the stratified mean catch tow^{-1}; CV = coefficient of variation for untransformed data; CV_{ln} = coefficient of variation for $\ln(x + 1)$ transformed data.

Cruise	n	$\bar{x}_{st}$	$\bar{x}_{ln}$	$\bar{x}_{Bliss}$	CV	CV_{ln}
Fall 1973 (23 Oct.-16 Nov.)	67	2.83	0.59	1.86	31.6	1.68
Spring 1974 (1 Apr.-9 May)	89	1.21	0.25	0.58	35.8	1.70
Summer 1974 (13 Aug.-19 Sept.)	69	3.13	0.59	1.97	25.5	1.69
Winter 1975 (16 Jan.-2 Feb.)	52	0.24	0.11	0.79	0.8	2.02
Spring 1975 (31 Mar.-10 Apr.)	40	0.08	0.06	0.07	0.4	1.31
Summer 1975 (30 Aug.-19 Sept.)	68	1.17	0.37	0.89	7.9	1.47
Winter 1976 (12 Jan.-7 Feb.)	69	1.73	0.17	0.52	62.4	2.81
Summer 1976 (28 Aug.-21 Sept.)	69	1.51	0.34	0.87	25.7	1.70
Winter 1977 (17 Jan.-9 Mar.)	72	3.30	0.14	1.18	197.0	9.01

abundance and distribution (Wenner et al. 1979a). All trawling was conducted from the RV *Dolphin*, a 32.6 m converted tug, for approximately 30 minutes at 6.5 km/hour. Weight and fork length (FL) were measured for each individual, except for large catches which were subsampled. Surface and bottom temperatures were taken after each tow.

Length-frequency distributions were compared by season and by depth zone. An index of relative abundance (IRA = $1/n \sum \ln(x + 1)$; n = # trawls in each depth zone, x = weight of fish for each tow) was calculated from the catches for each depth zone (Musick and McEachran 1972). The stratified mean catch per tow and the estimated variance of the stratified mean catch per tow (Cochran 1977) were calculated from untransformed and $\ln(x + 1)$ transformed data to reduce the effects of contagion (Elliott 1971). The coefficient of variation was used to compare variation in catches (Clark and Brown 1977). The Bliss (1967) approximation retransformed the data from logarithmic to arithmetic units. The Wilcoxon rank sum statistic (Hollander and Wolfe 1973) was used to compare catches, depths, and temperatures of sponge-coral (Wenner 1983) and sandy open-shelf (Struhsaker 1969) habitats. Habitat designations of Wenner et al. (1979a) were used. Catches collected north and south of lat. 31°30′N were compared for winter and summer cruises to determine if seasonal migration occurred.

Reproductive Biology

Specimens used for reproductive analyses were collected in 1980 by several research and commercial vessels, frozen, and examined in the laboratory. Specimens were measured (nearest mm) and weighed (nearest 0.1 g). Ripe ovaries were fixed in Gilson's solution (Bagenal and Braum 1978) for fecundity determination. All other gonads were fixed in formol-alcohol, stained with a modified Harris hematoxylin and counterstained with eosin (Humason 1972). Maturity stages for testes follow Hyder (1969); maturity stages for ovaries were based on Wallace and Selman (1981) and the frequency distributions of oocyte diameters. Frequency distributions of oocyte sizes were determined from randomly selected ovaries in each maturity stage. Analysis of variance revealed no differences in means and variances of oocyte diameters taken from different regions of ovaries in any stage. Therefore, oocyte distributions for each ovary were determined from two or three randomly selected sections.

Proportions of fish in each maturity stage were determined bimonthly, and gonadosomatic indices [GSI = gonad wt/(body wt – gonad wt)] were determined for each maturity stage (except stage 1 when gonadal tissues weighed <0.1 g).

Ova numbers were estimated by modifying the methods of Macer (1974). Both ripe ova and developing oocytes with diameters >0.115 mm were counted. Developing oocytes were included in fecundity estimation because they exhibited characteristics of secondary growth phase (Wallace and Selman 1981) and were atretic in spent ovaries.

Feeding Habits

Stomach contents of 457 fish collected in 1980 were fixed in 20% formalin, and stored in 50% isopropyl alcohol. Frequency of occurrence (%FO) and percentage composition by number (%N) were computed for major prey categories. Volumetric displacement (%VOL) of prey categories from a representative subsample of 30 stomachs were determined by using a 0.1 cm^2 grid (Windell 1971). Seasonal and ontogenetic change in diets were compared with an index of relative importance [IRI = (%N + %VOL)(%FO)], computed from the sums of each prey category (Pinkas et al. 1971).

Feeding periodicity was determined by plotting the percentage of empty stomachs collected per time period, using 377 stomachs with known collection times. Distributions of fish lengths collected in dif-

ferent time intervals were compared to evaluate size bias that may occur with this method (Jenkins and Green 1977).

Age and Growth

Utricular otoliths (lapilli) of specimens collected in 1980 were used for age determination. Otoliths were stored in 95% ethyl alcohol and prepared for viewing using a modification of the methods of Haake et al. (1981), which resulted in a thin sagittal section containing the core of the otolith embedded in "Spurr" (Spurr 1969). Otolith length was measured to the nearest 0.1 mm at 100× with an ocular micrometer. Otolith images were projected on a high resolution television screen with a high resolution camera, which produced a total viewing magnification of 1088× or 2176×. Otoliths examined by scanning electron microscopy were prepared by the methods of Haake et al. (1981). Two counts of growth increments were made by the author, and an additional count was made by other experienced readers. Mean counts were used in all analyses, and specimens were discarded if individual counts for a specimen differed by more than 10%. Different readers usually showed agreement between counts: percentage difference between readers averaged 8%.

Counts of otolith increments were obtained from 71 juvenile and adult round scad, 13-143 mm FL. Sixty specimens (121-180 mm FL) could not be assigned ages because of the numerous growth interruptions in outer regions of the otolith. Increment formation was validated by examination of the margins of otoliths of juveniles (13-55 mm FL) collected at different times of day. Consistent measurements of the marginal increment could not be made because of the irregular shape of the lapilli; thus, only the occurrence of an incremental or discontinuous zone (terminology of Mugiya et al. 1981) could be noted.

The SAS NLIN regression procedure with DUD and Marquardt options (Helwig and Council 1979) was used to determine parameters for the von Bertalanffy (1957) and Gompertz (Zweifel and Lasker 1976) growth equations. Because similar patterns of variation were observed in plots of the residuals of both models, r^2 values were used to evaluate model performance (Grossman et al. 1985). Instantaneous growth rates (%FL d^{-1} and %WT d^{-1}) were calculated according to Ricker (1979). Weights were converted from lengths by using the least squares regression (Sokal and Rohlf 1981), ln wt (in g) = 2.96 ln FL (in mm) − 11.2 (r^2 = 0.99), determined from 156 individuals (13-185 mm FL) randomly selected within 10 mm size classes from all specimens (total = 1047) collected in 1980.

RESULTS

Seasonal Distribution and Relative Abundance

A total of 57,460 round scad were captured at 230 of the 739 stations in depths from 11 to 267 m; over 99% of the catch came from <92 m. Fish ranged from 2 to 26 cm FL ($\bar{x}$ = 11.4), with 99% of the fish 6-17 cm FL.

Round scad were more widely distributed and abundant in summer and fall than in winter and spring. Indices of relative abundance (Fig. 1) were consistently high in summer and fall at shallow depths (<55 m) where *D. punctatus* were captured at 121 of 220 trawl stations. Indices of relative abundance during summer and fall in 56-110 m depths were quite variable, and catches in waters >110 m were rare (3 of 78 trawls), small (52 individuals captured), and occurred only in summer. The highest indices in winter and spring occurred in 19-110 m depths (usually 19-27 m), but were lower than values in summer and fall. Round scad were rarely collected in 9-18 m depths and never collected in waters >110 m in winter.

Differences among untransformed ($\bar{x}_{st}$), transformed ($\bar{x}_{\ln}$), and Bliss ($\bar{x}_{\text{Bliss}}$) estimates of the stratified mean catch per tow (Table 1) revealed additional seasonal changes in the distribution of round scad. Transformed and Bliss estimates of the stratified mean catch per tow were higher in summer and fall than in winter and spring. However, untransformed values ($\bar{x}_{st}$) indicated that total catches in winter often exceeded total catches in summer. Such differences in catch statistics resulted from the relatively high frequency and low variability of catches in summer and fall, and the relatively low frequency and high variability of catches in winter and spring. This result was generally consistent with the coefficients of variation (CV and $CV_{\ln}$), which indicated increased clumping in the winter catches.

The seasonal distribution of round scad appeared affected by temperature (Table 2). Over 97% of winter catches occurred in waters warmer than 15°C, over 99% of spring catches were made in waters warmer than 17°C, and over 99% of summer and fall catches occurred in waters warmer than 20°C.

Habitat affected the distribution of round scad in

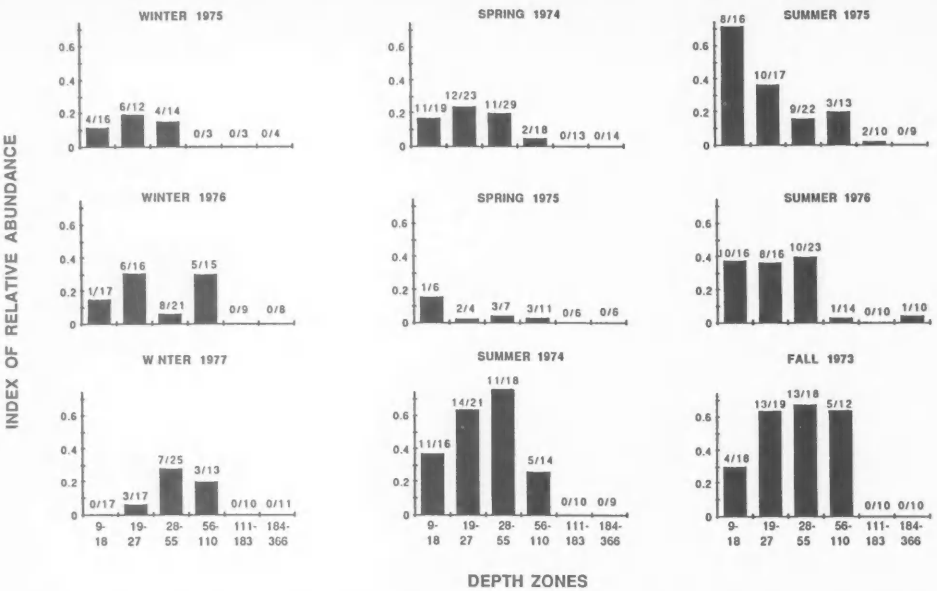

FIGURE 1.—Indices of relative abundance (Musick and McEachran 1972) of *Decapterus punctatus* by depth zone from MARMAP trawl survey for all cruises. Fractions are the number of trawls with round scad/total number of trawls.

TABLE 2.—Surface and bottom temperatures where *Decapterus punctatus* was collected in the South Atlantic Bight. Upper figure of each pair is surface value, lower figure is bottom value; $\bar{x}$ = mean, s = variance.

	Winter			Spring		Summer			Fall
	1975	1976	1977	1974	1975	1974	1975	1976	1973
$\bar{x}$	17.4	19.1	17.9	19.6	18.7	27.9	28.1	26.0	23.8
	17.2	17.0	16.4	19.1	17.4	25.5	25.4	25.4	23.7
s	2.5	3.5	2.5	1.5	2.7	0.5	0.6	0.6	1.9
	2.0	2.8	2.1	1.3	1.3	1.9	4.9	3.5	1.9
mini-	13.3	12.1	11.5	17.4	14.9	26.9	26.9	26.0	17.2
mum	13.3	12.3	11.6	17.0	14.9	19.3	9.8	8.5	17.2
maxi-	21.7	23.3	18.9	23.2	23.8	29.1	29.3	28.7	26.5
mum	19.9	22.8	18.9	22.0	19.2	28.2	29.2	27.4	26.3

winter. Catches over sponge-coral habitat were significantly larger than catches over sandy habitat in winter during 1976-77, whereas catches over the two bottom types were similar in other seasons (Table 3). Habitat types did not differ in temperature during either winter (Wilcoxon rank sum tests, P = 0.25 and 0.20, df = 19 and 12, respectively). Thus, temperature alone did not appear to account for the observed difference in winter catches over the two bottom types.

TABLE 3.—Comparison of catches of *Decapterus punctatus* over sponge-coral and sand habitats by cruise. If the Wilcoxon rank sum (Z) is significant (*), the direction of the difference is indicated. ΣC_l = sum of catches over sponge-coral habitats (n_l = # trawls), ΣC_s = sum of catches over sand habitats (n_s = trawls).

Cruise	ΣC_l	n_l	ΣC_S	n_s	Z	
Winter						
1975	3	(3)	672	(49)	0.23	
1976	7,201	(11)	597	(75)	3.57*	(L>S)
1977	10,936	(11)	39	(82)	5.40*	(L>S)
Spring						
1974	239	(11)	4,717	(91)	0.05	
1975	2	(6)	46	(34)	0.36	
Summer						
1974	445	(14)	8,023	(74)	0.61	
1975	614	(18)	4,805	(69)	0.92	
1976	663	(8)	5,094	(81)	0.86	
Fall						
1973	215	(10)	13,139	(77)	0.74	

Round scad did not appear to undertake seasonal longshore migrations in the South Atlantic Bight. Catches north and south of lat. 31°30'N (which roughly bisects the South Atlantic Bight) showed occasional differences (Table 4), but no consistent

seasonal pattern. Catch differences indicative of a southward migration in winter and northward in summer (either N < S in winter and spring or N > S in summer and fall) occurred only in winter 1975 and summer 1976. Distributions opposite to the above patterns occurred in summer 1975. Similarity in the numbers (Chi-square test, $P = 0.50$, 1 df) of gill rakers, a variable character (Berry 1969), from specimens collected off South Carolina in winter ($\bar{x} = 37.2$, $s^2 = 1.2$, $n = 33$) and summer ($\bar{x} = 36.9$, $s^2 = 1.4$, $n = 38$) also suggested that discrete stocks were not migrating through the South Atlantic Bight.

Although adults and juveniles were caught at all depths throughout the year, length-frequency distributions by depth (Fig. 2) showed a similar pattern for nearly every cruise: fish size decreased from 9-18 m to 19-27 m depths, then increased with increasing depth to 110 m. Catches in 9-18 m consisted primarily of adults in fall and winter, whereas both juveniles and adults were captured in spring and summer. Juveniles predominated in 19-27 m, whereas adults composed most of the catch in deeper waters.

TABLE 4.—Comparison of catches of *Decapterus punctatus* north and south of lat. 31°30′N by cruise. If the Wilcoxon rank sum (Z) is significantly different (*), the direction of the difference is indicated. ΣC_n = sum of the catches north (n_n = # trawls north), ΣC_s = sum of the catches south (n_s = # trawls south).

Cruise	ΣC_n	n_n	ΣC_s	n_s	Z	
Winter						
1975	8	(17)	667	(35)	561.80*	(S>N)
1976	6,149	(42)	1,649	(44)	0.07	
1977	10,728	(48)	247	(45)	0.31	
Spring						
1974	993	(62)	3,963	(40)	0.33	
1975	44	(36)	4	(4)	0.25	
Summer						
1974	1,892	(47)	6,576	(41)	0.15	
1975	1,915	(49)	3,504	(38)	1.35*	(S>N)
1976	4,395	(46)	1,362	(43)	2.52*	(N>S)
Fall						
1973	6,184	(47)	7,170	(40)	0.85	

Reproductive Biology

All stages of ovarian maturity had different frequency distributions of oocyte diameters (Fig. 3). Resting ovaries contained primary or first growth phase oocytes approximately 25-115 μm in diameter. Few larger (>115 μm) developing or atretic oocytes occurred. Oocytes in developing ovaries ranged from 30 to 375 μm in diameter, and exhibited characteristics of first or second growth phase. Either one or two modes were present in the frequency distributions of the sizes of second growth phase oocytes, 100-375 μm in diameter. Germ cells in ripe ovaries ranged from 30 to 495 μm in diameter. Ripe ovaries contained oocytes in both growth phases and maturing ova. Two or three modes were present in the frequency distibution of germ cells of ripe ovaries. Spent ovaries contained small oocytes in primary growth phase and occasionally larger oocytes undergoing atresia. Germ cells in these flaccid ovaries were usually 30-255 μm in diameter, although larger cells were observed. Gonadosomatic indices (Table 5) changed as expected: indices increased from resting through ripe stages, then decreased for spent fish.

Maturity stages of testes were more difficult to distinguish because testes often contained all stages of spermatogenesis; therefore, stage determination was based upon subjective interpretation of the relative quantities of spermatocytes, spermatids, and sperm. Although more variable, gonadosomatic indices of males (Table 5) were similar to those of females.

TABLE 5.—Gonadosomatic indices (gonad wt/(total body wt − gonad wt)) of *Decapterus punctatus* by stage maturity. $\bar{x}$ = mean, s = variance, n = sample size.

	Testes			Ovaries		
	$\bar{x}$	s	n	$\bar{x}$	s	n
Resting	0.008	0.004	64	0.007	0.003	60
Developing	0.018	0.012	103	0.027	0.011	49
Ripe	0.028	0.014	74	0.045	0.019	64
Spent	0.015	0.009	18	0.016	0.008	13

Seasonal occurrence of maturity stages showed good agreement between males and females (Fig. 4), and indicated a protracted spawning period. Developing gonads were found from February through August, and ripe individuals of both sexes were collected from March through August.

Examination of gonads indicated that both species mature at approximately 110 mm FL. Frequency distributions of length by sex (Fig. 5) indicate that both sexes mature over a narrow size range. Specimens <100 mm FL were immature, whereas more than 90% of fish 110-119 mm FL were mature. Both ripe males and females were collected in the size range at which gonadal development begins (100-109 mm FL).

Fecundity estimates (# ova female^{-1} yr^{-1}) for 32 ripe females (119-174 mm FL) ranged from 6,200 to 51,000 per female and were highly variable for specimens of similar sizes. The distribution of the sizes of the oocytes in these ovaries was not deter-

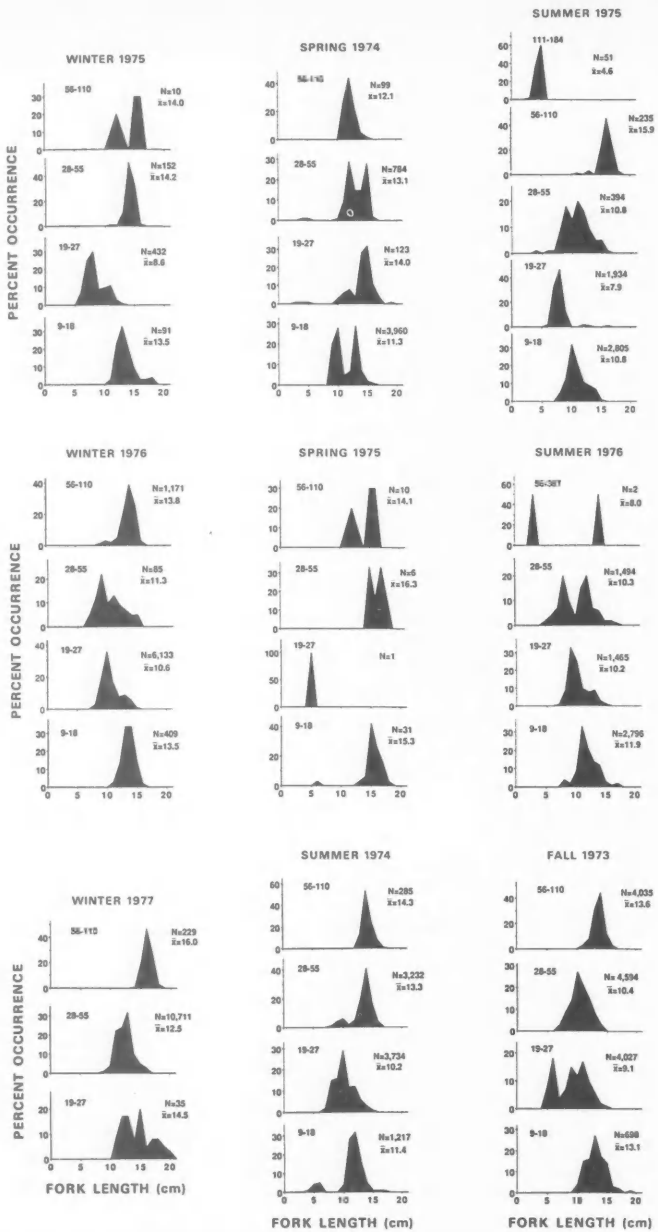

FIGURE 2.—Frequency distributions of fork lengths of *Decapterus punctatus* by depth zone, for all cruises. Numbers above each distribution indicate range of the depth zone in m; N is sample size; $\bar{x}$ is mean length of individuals.

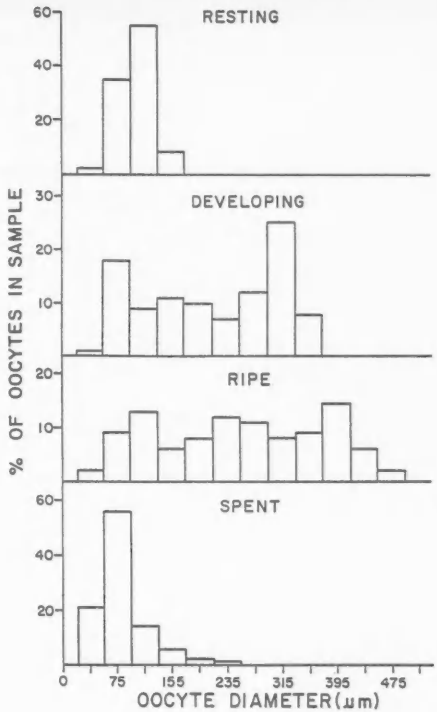

FIGURE 3.—Frequency distributions of oocyte diameters from four randomly selected ovaries of *Decapterus punctatus* in each maturity stage. The total number of oocytes measured in each ovary was 306 (oocytes from 3 sections within the anterior, central, and posterior regions of each ovary).

mined, and it was unknown if these individuals had spawned. The regression equations of fecundity on length and weight for 33 specimens were as follows: $\log_{10}$ fec = −10.9 + 5.63 $\log_{10}$ FL (r^2 = 0.46); and $\log_{10}$ fec = −1.14 + 1.56 $\log_{10}$ wt (r^2 = 0.55).

Feeding Habits

Approximately 91% of round scad (39-189 mm FL) contained identifiable prey. The highest indices of relative importance for all specimens were for copepods (0.37), mollusk larvae (0.19), amphipods (0.06), and ostracods (0.04). The most numerous prey groups were mollusk larvae (29%, predominantly gastropod and pelecypod veligers), copepods (25%), barnacle cyprids (14%), and ostracods (10%). Chaetognaths (35%), copepods (28%), mollusk larvae

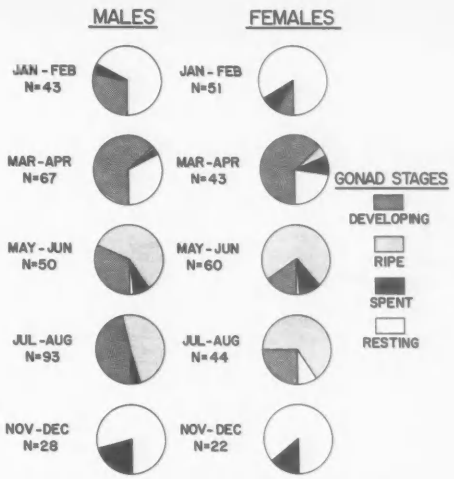

FIGURE 4.—Seasonal occurrence of maturity stages of gonads of *Decapterus punctatus*. N is sample size for each bimonthly period. No gonads were examined from specimens collected in September and October 1980-81.

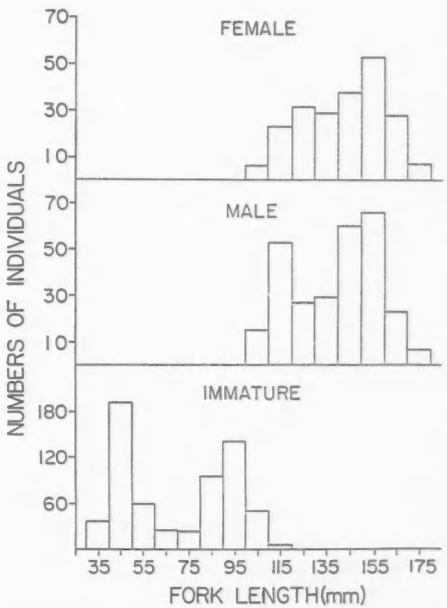

FIGURE 5.—Frequency distributions of fork length of *Decapterus punctatus* by sex. Both sexes mature at approximately 110 mm FL.

(12%), and amphipods (10%, predominantly hyperiids and caprellids) contributed the greatest volumes of prey. Copepods (70%), mollusk larvae (47%), amphipods (30%), and decapod larvae (25%) occurred most frequently.

Some differences were found in stomach contents of fishes of different size (Table 6). Small fish preyed almost exclusively on copepods. Medium-sized fish preyed predominantly on copepods, but less frequently and to a lesser extent than small fishes. Large fish fed on a variety of prey and consumed large prey items (such as chaetognaths).

Mollusk larvae and copepods dominated the diets in all seasons except spring (Table 7). In spring, round scad fed on copepods, ostracods, chaetognaths, and barnacle cyprids. The preponderance of copepods in diets of round scad in summer is due in part to the large number of juveniles included in the analysis. The mean size of fish in the summer sample was smaller than the mean size of fish in all other seasons (Student-Newman-Keuls tests; $q_{453,4}$ = 14.1 for winter vs. summer, $q_{453,3}$ = 13.2 for summer vs. spring, and $q_{453,2}$ = 11.1 for summer vs. fall). In all other seasons, dietary analyses (Table 5) were based on fish samples with similar size distributions (Student-Newman-Keuls tests; $q_{453,3}$ = 0.7 for winter vs. fall, $q_{453,2}$ = 0.7 for winter vs. spring, and $q_{453,2}$ = 0.1 for fall vs. spring). The mean number of prey items showed considerable seasonal variation from 4.6 in fall to 104 in spring.

The percentage of empty stomachs varied as a function of time of day (Fig. 6). Few empty stomachs (2-7%) were collected from midmorning to early evening, whereas 13-29% of stomachs were empty from early evening to midmorning. Size effects are unlikely to have caused the observed differences in the percentages of empty stomachs: samples with lower (2, 5, and 7) and higher (13, 20, and 29) percentages were comprised of fish of similar size (ANOVA, $F_{(1,4)} \doteq 0.01$, $P > 0.75$).

Age and Growth

Validation of the daily growth marks on otoliths of round scad was provided in two ways. Examination of marginal increments of lapilli from small specimens (13-55 mm FL) collected at different times of day suggested daily periodicity of increment formation. The margin consisted of the transparent incremental zone from midafternoon until early morning and the dark discontinuous zone in midmorning (Table 8). The allometric relationship between otolith and fish length also validates the use of otoliths for age determination. Otolith length (OL)

TABLE 6.—Index of relative importance (IRI), frequency of occurrence (%FO), volumetric displacement (%VOL), and relative abundance of prey (%*N*) by sizes. N = sample size (# empty stomachs), $\bar{x}$ = mean fork length in mm, s = variance of fork lengths, and n = total number of prey.

Length/prey	*N* %	VOL %	FO %	IRI
40-89 mm FL: N = 82(12), $\bar{x}$ = 50 mm, s = 13 mm, n = 1,272				
Copepoda	74	80	75	1.15
Mollusca	13	5	24	0.04
Decapoda	3	7	27	0.03
Amphipoda	2	2	15	0.01
Eggs	3	2	24	0.01
Ostracoda	1	1	10	<0.01
Other	4	3	32	0.02
90-139 mm FL: N = 192(15), $\bar{x}$ = 114 mm, s = 13 mm, n = 8,003				
Copepoda	34	57	74	0.67
Mollusca	20	13	47	0.16
Cirripedia	31	13	20	0.09
Ostracoda	9	8	22	0.04
Amphipoda	2	3	28	0.01
Decapoda	1	3	25	0.01
Other	3	3	32	0.02
140-189 mm FL: N = 183(14), $\bar{x}$ = 156 mm, s = 10 mm, n = 12,850				
Mollusca	36	12	59	0.28
Copepoda	14	12	64	0.17
Amphipoda	14	12	31	0.08
Chaetognatha	15	53	10	0.07
Ostracoda	11	5	30	0.05
Cirripedia	4	2	25	0.02
Decapoda	1	1	32	0.01
Other	5	4	48	0.04

TABLE 7.—Frequency of occurrence, volumetric displacement, and relative abundance of prey of *Decapterus punctatus* by season. Abbreviations as in Table 6; r = range of fork lengths.

Season/prey	N %	VOL %	FO %	IRI
Winter: N = 116(10), $\bar{x}$ = 140 mm, s = 25 mm, r = 85-185 mm, n = 4,357				
Mollusca	47	32	48	0.38
Copepoda	17	31	52	0.25
Ostracoda	15	14	31	0.09
Cirripedia	12	5	33	0.06
Decapoda	2	7	35	0.03
Amphipoda	1	2	17	0.01
Other	6	9	47	0.07
Spring: N = 112(5), $\bar{x}$ = 135 mm, s = 18 mm, r = 97-175 mm, n = 10,999				
Copepoda	21	18	92	0.36
Amphipoda	17	15	52	0.16
Ostracoda	13	6	45	0.09
Chaetognatha	17	51	13	0.09
Cirripedia	22	5	25	0.07
Mollusca	6	2	67	0.05
Decapoda	1	2	26	0.01
Other	3	2	45	0.02
Summer: N = 161(16), $\bar{x}$ = 87 mm, s = 40 mm, r = 35-163 mm, n = 6,505				
Copepoda	55	73	79	1.01
Mollusca	37	18	43	0.24
Decapoda	1	3	22	0.01
Amphipoda	1	1	21	<0.01
Ostracoda	1	1	10	<0.01
Cirripedia	1	1	9	<0.01
Other	2	2	28	0.01
Fall: N = 68(10), $\bar{x}$ = 138 mm, s = 33 mm, r = 48-180 mm, n = 264				
Mollusca	65	44	21	0.23
Copepoda	19	34	42	0.22
Other	16	22	36	0.14

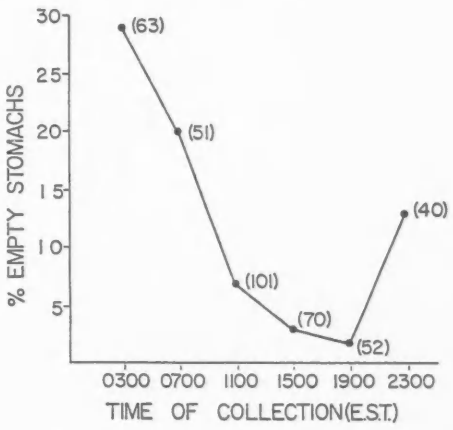

FIGURE 6.—Percent of empty stomachs of *Decapterus punctatus* collected at different times of day. Samples were pooled over 4-h intervals, of which midpoints are given. (n) is sample size.

TABLE 8.—Appearance of marginal increments of otoliths of *Decapterus punctatus* collected at different times of day. Data indicate increments are formed daily. N = number of specimens, times are Eastern Standard Time.

FL of specimens (N)	Time of capture	Marginal increment
42-55 mm (4)	0239-0257	wide, transparent
17-22 mm (11)	0812-0817	thin, dark
13-24 mm (4)	1506-1516	wide, transparent
35-53 mm (8)	2045-2053	wide, transparent

was proportional to fork length throughout the size range (14-143 mm FL) for which age determination was possible ($\log_{10}$ OL (in mm) = 0.82 $\log_{10}$ FL (in mm) − 1.61; r^2 = 0.99, n = 71).

The thickness and structure of growth increments changed in consistent ways in lapilli (Fig. 7). Ten to twelve faint daily increments surrounded a central core, which contained the primordium (Fig. 8). The next 10-15 increments increased in thickness, and the following 20-25 increments gradually decreased in thickness. A distinct change occurred at this point, and increments became thinner and more regular. Increments appeared uniform in thickness

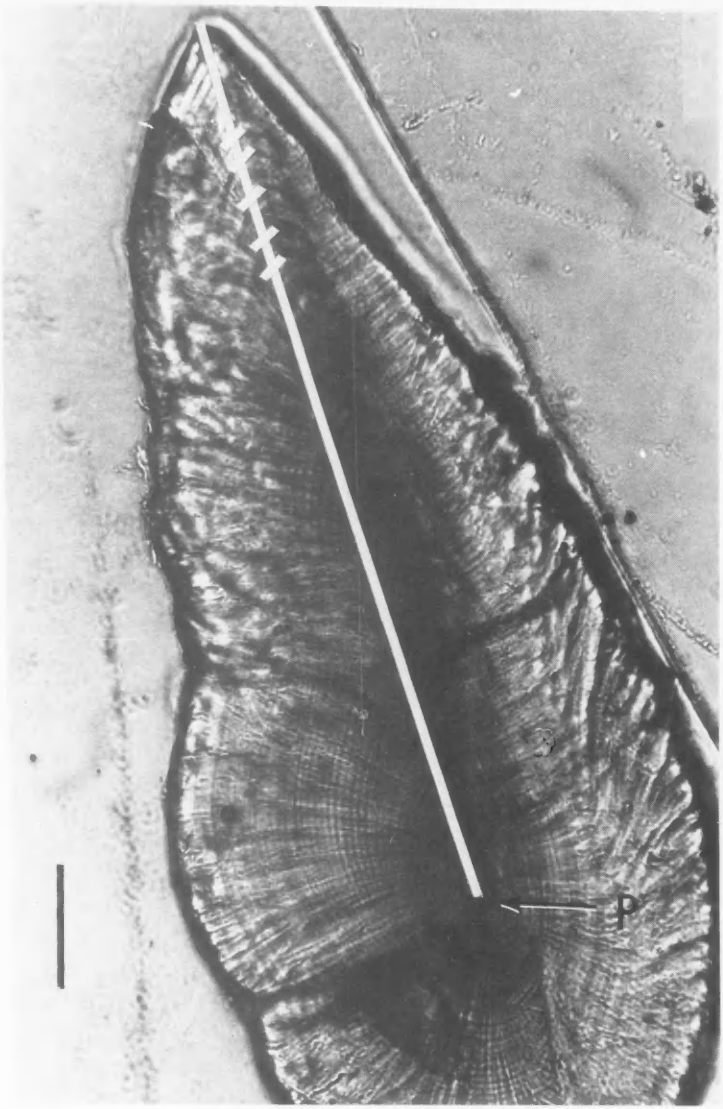

FIGURE 7.—Sagittal section through a lapillus of *Decapterus punctatus*. The pattern of fine, regular growth increments is interspersed increasingly with heavy, irregular growth interruptions (crosshatches) in outer regions of the otolith. Bar indicates 0.10 mm, P is the primordium.

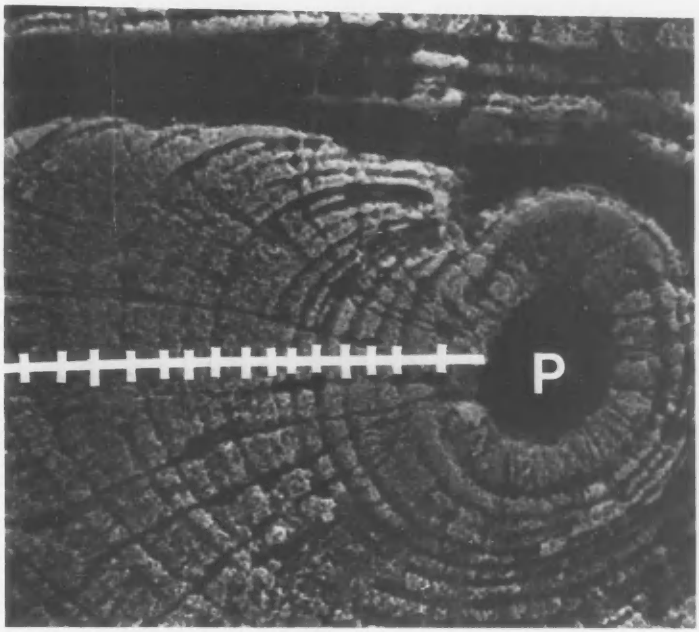

FIGURE 8.—Scanning electron micrograph of a sagittal section through the primordium of a lapillus of *Decapterus punctatus*. P is the primordium and crosshatches denote daily increments. The pattern of otolith growth of juveniles was consistent in most otoliths.

to approximately increment 100, then gradually became thinner and more difficult to count. Growth interruptions appeared in outer portions of otoliths of large fish, and growth records were more irregular.

Round scad grew rapidly for 120-150 days until reaching sexual maturity at approximately 110 mm FL (Fig. 9). The von Bertalanffy [FL = 161 (1 – exp (–0.012 (age – 29.5)))] and Gompertz [FL = 1.17 exp [4.76 (1 – $e^{-0.026\,(age)}$)]] growth equations provided good and nearly identical fits (r^2 = 0.96 and 0.97, respectively) to the observed data. Specific growth rates (Table 9) for juveniles were initially high, decreased sharply until sexual maturity, then decreased more gradually throughout the time period for which age determination was possible. The largest specimen for which reliable counts could be determined was 143 mm FL, although most specimens at that size could not be assigned an age.

The age of round scad for the entire size range (FL up to 21 cm) that was collected in the South Atlantic Bight could not be determined from daily increments on the lapillus. The age of all specimens <120 mm FL could be determined, but only half of

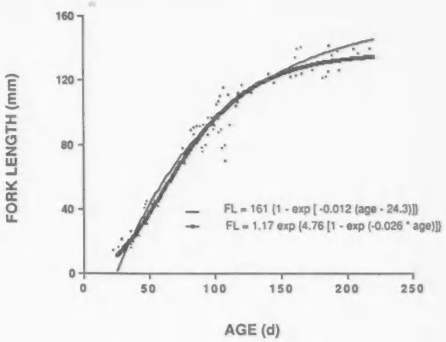

FIGURE 9.—Von Bertalanffy (thin line) and Gompertz (heavy line) growth equations. Sexual maturity of *Decapterus punctatus* is reached at approximately 110 mm FL in 120-150 days.

TABLE 9.—Instantaneous growth rates (Ricker 1979) of *Decapterus punctatus* predicted from the von Bertalanffy equation (fig. 11). Weights were converted from lengths by using the regression: ln Wt (g) = 2.96 ln FL (mm) − 11.2.

Age (d)	FL d^{-1} (%)	Wt d^{-1} (%)
35-60	6.3	13.2
61-85	1.9	5.6
86-105	0.8	2.6
106-130	0.7	2.2
131-155	0.4	1.6
156-180	0.3	1.2

the specimens 121-143 mm FL and no individuals >143 mm FL could be assigned an age. Replicate counts of otolith increments from adults often differed by >10%, and were considered unreliable. In addition, frequent growth interruptions occurred in the outer portions of the otoliths of large specimens, and the timing of formation of such marks was not known.

DISCUSSION

Seasonal Distribution and Relative Abundance

Round scad apparently migrate shoreward across the continental shelf as sea temperatures increase in spring, then migrate into warm (>15°C) midshelf (28-110 m) depths as inshore temperatures decline in winter. Intermediate shelf depths in the South Atlantic Bight are fairly warm year round, unlike inshore waters which are seasonally cooled by cold fronts (Atkinson et al. 1983) and outer shelf waters which are intruded upon by cold-water upwellings (Blanton et al. 1981). Magnuson et al. (1981) reported that catches of round scad were proportional to temperature, and laboratory studies (Wyllie et al. 1976) have suggested a preferred temperature of 27°C. Seasonal onshore and offshore movements are made by round scad in the Gulf of Mexico (Klima 1971) and by other pelagic fishes in the South Atlantic Bight (Wenner et al. 1979a, b, c, d, 1980) and elsewhere (Allen and DeMartini 1983).

Longshore migration does not appear to be a consistent feature of the movements of round scad along the southeastern Atlantic states. Differences of catches (Table 4) made north and south of lat. 31°30′N are inconsistent, and limited meristic data (see Results) provides no evidence of movements by discrete stocks through the South Atlantic Bight. Although fish communities of live bottom habitats may change (Chester et al. 1984), latitudinal differences in the distribution of demersal fishes in sandy, open shelf habitats of the South Atlantic Bight are not apparent (Wenner et al. 1979a). More substantive information (tag-recapture studies, etc.) than the limited data given above is needed to determine accurately the movement patterns of round scad. At the present time, available information suggests that seasonal migration in round scad involves mainly onshore or offshore movement.

The abundance of round scad in the South Atlantic Bight is undoubtedly underestimated by catch statistics (Table 2). First, benthic otter trawling is generally inadequate for determining the abundance of small, mobile pelagic species (Wenner et al. 1979a). Second, the attraction of round scad to sponge-coral habitats in winter may have exaggerated the apparently large fluctuations in the seasonal abundance of round scad in the South Atlantic Bight. The sampling protocol assumes equal probability of capture over the different habitat types, but the probability of capturing round scad over live-bottom habitats varies seasonally. An increased proportion of live-bottom areas should be sampled in winter to obtain more reliable estimates of the abundance of round scad. The distribution, extent, and adequacy of sampling of live-bottom habitats are not well known (Wenner 1983). Thus, sampling inadequacies and the seasonal attraction of round scad to live-bottom habitat result in underestimation of abundance.

Several factors may influence the attraction of round scad to live-bottom habitat in winter. First, round scad utilize live-bottom habitat in winter, when invertebrate biomass has peaked and potential competitors and predators have decreased (George and Staiger 1978[3]; Wenner et al. 1980, 1983, 1984; Sedberry and Van Dolah 1984). Second, winter temperatures at live-bottom stations, though not significantly different from temperatures at sand-bottom stations, tend to be warmer, and scad prefer warm waters. The greatest densities of round scad occur in the midshelf where seasonal temperatures are generally warmest and the most highly productive live-bottom areas are located (Miller and Richards 1980; Sedberry and Van Dolah 1984). Finally, the relief of live-bottom habitats (albeit low) may serve to attract round scad; many coastal pelagic fishes, including round scad, have an affin-

[3]George, R. V., and J. C. Staiger. 1978. Epifaunal benthic invertebrate and demersal fish populations in the Georgia Bight continental shelf environment. South Atlantic Benchmark program, Volume 3, Texas Instruments Inc. Draft Report, p. 211-254.

ity for structure (Klima and Wickham 1971; Feder et al. 1974; Hastings et al. 1976).

Although fish sizes within each depth zone overlapped, the observed pattern was fairly consistent and distinct for all cruises; adults composed the catch in 9-18 m depths, and fish in deeper waters (mostly juveniles) showed a positive size-depth correlation. Adults migrate inshore in spring to feed and spawn, and offshore in winter to avoid cold waters. However, the apparent movement of juveniles to deeper waters is not understood. Correlations between fish size and depth are numerous in aquatic habitats (Helfman 1978), but explanations based on changing physiological tolerances (Bullis and Struhsaker 1970), foraging strategies (Polloni et al. 1979), and predation responses (Hobson 1972) have been difficult to demonstrate in most fishes.

Reproductive Biology

Although results (Fig. 3) indicate that *D. punctatus* spawn primarily from March through August, spawning probably occurs through September and to a lesser extent throughout the year. Collections were not made during September and October of 1980, but water temperatures in August and September in the South Atlantic Bight are generally similar (Atkinson et al. 1983). Round scad larvae have been collected in winter in the South Atlantic Bight (Fahay 1975; Powles and Stender 1976) and the eastern Gulf of Mexico (Leak 1981). Larval occurrence has been correlated with water temperature in the eastern Gulf of Mexico (Leak 1981), and sufficient water temperatures (>20°C) occur throughout the year in parts of the South Atlantic Bight.

The pattern of oocyte development is generally quite variable and complex in serial spawners: oocytes develop asynchronously or synchronously in groups, and ova are released in batches. Three observations suggested that round scad are serial spawners: 1) the occurrence of three distinct modes in the frequency distributions of oocyte diameters from ripe ovaries collected in spring; 2) two modes in those distributions from ripe fish collected in late summer; and 3) evidence of spawning in ovaries having a frequency distribution of oocyte diameters similar to developing ovaries. Spawning was indicated by disorganized ovarian septa with conspicuous spaces, debris in the ovarian lumen, residual atretic oocytes, and brown bodies.

Although estimates of fecundity in round scad are comparable to those of *D. pinnulatus* (Yamaguchi 1953), *D. macrosoma*, and *D. russelli* of similar size (Tiews et al. 1970), the conventional method applied here probably underestimated fecundity. Because gonads used in fecundity estimation were not examined histologically, it was not possible to determine if spawning had occurred recently in specimens used for fecundity measures. In addition, sufficient numbers of specimens were not examined to determine spawning frequency from running-ripe (DeMartini and Fountain 1981) or postovulatory (Hunter and Goldberg 1979) females. Previous studies on other serial spawning fishes (Hunter and Goldberg 1979; Hunter and Leong 1981; DeMartini and Fountain 1981; Conover 1985) have shown that estimates of annual fecundity (total number of ova spawned in 1 year) can differ from conventional fecundity estimates (which ignore multiple spawning) by an order of magnitude. Serial spawning fishes generally have low relative ovary weights (Martinez and Houde 1975; Smith and Lasker 1978; DeMartini and Fountain 1981), but can expend over 100% of their body weight per year in eggs (Hubbs 1976; DeMartini and Fountain 1981). If observed fecundity in round scad (6,200-51,000) is extrapolated from the 4.3% relative ovary weight (Table 7) to total body weight, then fecundity estimates of 142,000-1,173,000 would result. If observed fecundity is divided by the proportion of oocytes in the most advanced developmental mode (32%, from Figure 3), then batch fecundities of approximately 2,000-16,000 per female (130-230 eggs/g body weight) and annual fecundity estimates (based on 10 d spawning cycle for 6 months) of 36,000-288,000 would result. Both estimates are entirely speculative, but support the contention that the conventional method underestimated fecundity, and emphasize the need for additional studies on the fecundity of round scad.

Round scad mature at a smaller size than reported for other species of *Decapterus*, which reach maturity at 18-20 cm (Yamaguchi 1953; Tiews et al. 1970). The small size at which round scad become sexually mature suggests that they are under strong selection pressure to mature rapidly. The natural mortality of round scad in the eastern Gulf of Mexico is high (Houde et al. 1983). Compared with temperate and boreal species, many tropical clupeoids also mature at small sizes, seldom attain large size and have high adult mortality rates (Blaxter and Hunter 1982; Houde et al. 1983).

Feeding Habits

Zooplanktivores feed during the day or at night, but seldom during both periods (de Silva 1973; Hob-

son and Chess 1976; Helfman 1986), probably due to visual limitations (Durbin 1979). The absence of nocturnal prey and the strongly diurnal periodicity of stomach fullness (Fig. 6) indicate that *D. punctatus* feeds during the day. Round scad rarely consumed mysids, tanaids, and cumaceans, which are abundant in the water column at night but dwell in the benthos during the day (Kaestner 1970; Hobson and Chess 1976). The diel periodicity in empty stomachs (Fig. 6) is not biased by sizes of fish differing among collection times (see Results). Individuals of different sizes have similar gut evacuation rates (Perrson 1981) but different gut capacities; therefore, small individuals empty their guts more quickly than large individuals. The lack of a size difference in this analysis substantiates the daily feeding period by round scad.

Scales were a common item in round scad stomachs, but were deleted from analyses because several observations indicated that round scad were feeding on debris (including scales) generated by trawling: 1) oral chambers of specimens often contained scales; 2) scale size and type varied; and 3) the extent of presumed lepidophagy was not correlated with fish size. In addition, scales were seldom found in latter portions of the gut. Most other lepidophages generally prey on a small number of species (Sazima 1983), or for only a portion of their life history (Carr and Adams 1972). Thus, round scad probably consume scales on occasion, but not to the extent that the data would indicate. It seems likely that round scad were feeding on scales abraded from fishes during their avoidance of or capture by the trawl. Yamaguchi (1953) also attributed the occurrence of scales in the stomachs of *D. pinnulatus* to gear bias.

Ontogenetic changes in the diet occurred with growth. Larger individuals had more diverse diets which included larger prey. Small fish fed primarily on small, abundant copepods and copepodites. Stomach contents of several (10) small juveniles (13-26 mm FL) collected during an ichthyoplankton survey in 1973 also contained mostly copepods (S. Hales pers. obs.). Data from these specimens were not included in previous analyses due to the possibility of differential prey digestion.

Seasonal changes in the diets of round scad probably reflect fish size and the relative abundance of zooplankton components. Copepods and mollusks were the most important prey in all seasons except during spring when barnacle cyprids were the most numerous and chaetognaths contributed the greatest volume of prey. Zooplankton volumes and diversity reach their peak in the spring (Deevey 1960; Reeve 1964), and cyprids are more abundant in the spring than in any other season (Lang and Ackenhausen-Johns 1981). The preponderance of copepods in the diet of round scad in summer partially reflects the abundance of juvenile round scad, which appear to feed primarily on small abundant copepods.

Molluscan veligers may be an exception to the general pattern of prey selection. They have not been reported to be abundant in the zooplankton of the South Atlantic Bight (Paffenhöfer 1980, 1981) or elsewhere (Deevey 1960; Reeve 1964), yet occurred frequently in the diets of round scad. Shells of both gastropods and bivalves and the opercula of gastropods were all that remained in the stomachs of round scad on occasion; such parts are apparently digested slowly and retained in the stomach. However, such an explanation alone does not account for the frequency and abundance of mollusk veligers. Brewer and Kleppel (1986) have reported the paradox of low bivalve density yet frequent occurrence in the guts of some larval fishes, and suggested that bivalve veligers may occur in microscale patches just above the bottom. Planktonic stages of gastropods are important prey for horse mackerel (*Trachurus trachurus*), which school near the bottom (Macer 1977). Thus, the frequency and abundance of mollusk veligers in the stomachs of round scad may be attributed to both the abundance of mollusk veligers being greater than generally recognized and their low digestibility and long retention in stomachs.

Age and Growth

Round scad grow rapidly to sexual maturity at 11 cm FL in 4-5 months, and apparently achieve a major proportion of their total size in their first year. Because of the problems encountered in age determination in this study, little can be said about the age of most adults. The asymptote predicted by the von Bertalanffy model (161 mm FL) is much shorter than the maximum size observed in the South Atlantic Bight. Thus, the growth rates observed in this study should not be extrapolated to older and larger fish. Houde et al. (1983) reported the mean size of round scad in the eastern Gulf of Mexico to be 136 mm FL at age 1, 160 mm FL at age 2, and 177 mm FL at age 3. In addition, they reported considerable variation (10-20 mm) in the mean lengths at age. Differences in the growth rates observed in the two studies are believed to be due mainly to methodology, but may also be due to slight differences in the growth of round scad between the two areas.

Growth rates reported in this study for juvenile round scad are similar to those of juvenile *Selar crumenopthalmus* (Kawamoto 1973) and *Trachurus trachurus* (Macer 1977), and would enable spring-spawned round scad encountering favorable conditions to spawn in the fall (Leak 1981). Other species of *Decapterus* are reported to grow more slowly (Yamaguchi 1953; Tiews et al. 1970; Ingles and Pauly 1984), but such studies used length-frequency information only and may have underestimated growth. These species (*D. pinnulatus*, *D. russelli*, *D. macrosoma*) reach sexual maturity at 17-20 cm FL in their first or second year, and attain 25-35 cm FL in 3-5 years (Yamaguchi 1953, Tiews et al. 1970). The rapid growth of round scad to sexual maturity suggests that this species is under strong selection to mature early. Mortality estimates for round scad (Leak 1981; Houde et al. 1983) are high even in comparison with other coastal pelagic fishes, which do not achieve as large a size as round scad during their first year.

Daily growth increments were easily distinguished in juveniles and small adults, but could not be used to determine ages of most adults. Frequent spawning involving the high energetic expenditures reported for other pelagic fishes (Hubbs 1976; DeMartini and Fountain 1981) would result in slow growth of adults. Specific growth rates based on Houde et al. (1983) (0.04% FL d^{-1} for 1-2 yr olds, and 0.03% FL d^{-1} for 2-3 yr olds) are much slower than the rate of young adults (0.28% FL d^{-1}) observed in this study. A reduction in increment thickness with growth (Brothers 1979; Campana 1985) might result in the exceedingly fine increments observed in the outer portions of the otoliths of adults. Another possibility is that growth of adults is insufficient to maintain the pattern of daily increment formation. McGurk (1984) has reported that daily increment formation in larval *Clupea harengus* may be altered when absolute growth rates are <0.36 mm d^{-1}.

Occurrence of growth interruptions in the outer portions of otoliths of most adults also hindered age determination. The period of formation of such marks was not known. If such marks are not formed in 1 day, then inclusion of such marks as daily increments would result in underestimation of the ages of adults. Growth interruptions may result from spawning (Panella 1974), lunar or tidal rhythms (Rosenberg 1982), or stress (Ralston and Miyamato 1983); however, correlations between such events and the growth record of round scad could not be determined.

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LITERATURE CITED

AKAOKA, T.
1971. The purse seine fishery in Japan. *In* H. Kristjonsson (editor), Modern fishing gear of the world, Vol. III, p. 161-163. Fishing News Ltd., Lond.

ALLEN, L. G., AND E. E. DEMARTINI.
1983. Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre-Oceanside, California. Fish. Bull., U.S. 81:569-586.

APRIETO, V. L.
1974. Early development of five carangid fishes in the Gulf of Mexico and the south Atlantic coast of the United States. Fish. Bull., U.S. 72:415-444.

ATKINSON, L. P., T. N. LEE, J. O. BLANTON, AND W. S. CHANDLER.
1983. Climatology of the southeastern United States continental shelf waters. J. Geophys. Res. 88:4705-4718.

BAGENAL, T. B., AND E. BRAUM.
1978. Eggs and early life history. *In* T. B. Bagenal (editor), Methods for assessment of fish production in fresh waters, p. 165-201. Blackwell Sci. Publ., Lond.

BERRY, F. H.
1968. A new species of carangid fish (*Decapterus tabl*) from the western Atlantic. Contrib. Mar. Sci. 13:145-167.

BLANTON, J. O., L. P. ATKINSON, L. J. PIETRAFESA, AND T. N. LEE.
1981. The intrusion of Gulf Stream water across the continental shelf due to topographically induced upwelling. Deep-Sea Res. 28:393-405.

BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of clupeoid fishes. Adv. Mar. Biol., Acad. Press, N.Y., 20:1-224.

BLISS, C. I.
1967. Statistics in biology, Vol. I. McGraw Hill, N.Y., 558 p.
BOELY, T., A. WYSOKINSKI, AND J. ELWERTOWSKI.
1973. Les chinchards des cotes Senegaloises et Mauritaniennes. [In Fr.] Trav. Doc. ORSTOM Dakar-Thiaroze 43, 74 p.
BREWER, G. D., AND G. S. KLEPPEL.
1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217-226.
BROTHERS, E. B.
1979. Age and growth studies on tropical fishes. *In* S. B. Saila and P. M. Roedel (editors), Stock assessment for tropical small-scale fisheries, p. 119-135. Univ. Press, Kingston, RI.
BULLIS, H., AND P. STRUHSAKER.
1970. Fish fauna of the western Caribbean upper slope. Q. J. Fla. Acad. Sci. 33:43-76.
CAMPANA, S. E.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014-1032.
CARR, W. E. S., AND C. A. ADAMS.
1972. Food habits of juvenile marine fishes: evidence of the cleaning habit in the leatherjacket, *Oligoplites saurus*, and the spottail pinfish, *Diplodus holbrooki*. Fish. Bull., U.S. 70:1111-1120.
CHESTER, A. J., HUNTSMAN, G. R., TESTER, P. A., AND C. S. MANOOCH, III.
1984. South Atlantic Bight reef fish communities as represented in hook-and-line catches. Bull. Mar. Sci. 34:267-279.
CLARK, S. H., AND B. E. BROWN.
1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel survey data. Fish. Bull., U.S. 75:1-21.
COCHRAN, W. C.
1977. Sampling Techniques. John Wiley and Sons, N.Y., 229 p.
CONOVER, D. O.
1985. Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: the Atlantic silverside *Menidia menidia*. Fish. Bull., U.S. 83:331-341.
DEEVEY, G. B.
1960. Plankton studies. Bull. Bingham Oceanogr. Collect., Yale Univ. 17:1-86.
DEMARTINI, E. E., AND R. K. FOUNTAIN.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547-560.
DE SILVA, S. S.
1973. Food and feeding habits of the herring *Clupea harengus* and sprat *C. sprattus* in inshore waters of the westcoast of Scotland. Mar. Biol. (Berl.) 5:689-705.
DURBIN, A. G.
1979. Food selection by plankton feeding fishes. *In* H. Clepper (editor), Predator-prey systems in fishery management, p. 203-218. Sport Fishing Inst., Wash., D.C.
ELLIOTT, J. M.
1971. Statistical analysis of samples of benthic invertebrates. Freshwater Biological Association of the United Kingdom, Publication #25, 144 p.
FAHAY, M. P.
1085. An annotated list of larval and juvenile fishes captured with surface-towed meter nets in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.
FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in Southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.
GROSSLEIN, M. D.
1969. Groundfish survey of the Bureau of Commercial Fisheries, Woods Hole. Commer. Fish. Rev. 31(7):22-35.
GROSSMAN, G. D., M. J. HARRIS, AND J. E. HIGHTOWER.
1985. The relationship between tilefish, *Lopholatilus chamaeleonticeps*, abundance and sediment composition off Georgia. Fish. Bull., U.S. 83:443-447.
HAAKE, P. W., C. A. WILSON, AND J. M. DEAN.
1981. A technique for the examination of otoliths by SEM with application to larval fishes. *In* C. F. Bryan, J. V. Conner, and F. M. Truesdale (editors), Proc. 5th Annu. Larval Fish Conf., p. 12-15. Louisiana State Univ. Press, Baton Rouge, LA.
HASTINGS, R. W., L. H. OGREN, AND M. T. MABRY.
1976. Observations on the fish fauna associated with offshore platforms in the northeastern Gulf of Mexico. Fish. Bull., U.S. 74:387-402.
HELFMAN, G. S.
1978. Patterns of community structure in fishes: summary and overview. Environ. Biol. Fishes 3:129-147.
1986. Fish behaviour by day, night, and twilight. *In* T. J. Pitcher (editor), The behaviour of teleost fishes, p. 366-387. Croom-Helm, Lond.
HELWIG, J. T., AND K. A. COUNCIL (editors).
1979. SAS Users Guide. SAS Institute, Inc., Carey, NC, 294 p.
HOBSON, E. S.
1972. Activity of Hawaiian reef fishes during evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-750.
HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.
HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. John Wiley and Sons, N.Y., 503 p.
HOUDE, E. D., C. GRALL, AND S. A. BERKELEY.
1983. Population parameter estimates for three shoaling pelagic fishes in the eastern Gulf of Mexico. Int. Counc. Explor. Sea, C.M. 1983/H:43, 11 p.
HUBBS, C.
1976. Diel reproductive pattern and fecundity of *Menidia audens*. Copeia 1976:386-388.
HUMASON, G. L.
1972. Animal tissue techniques. 2d ed. W. H. Freeman and Co., San Franc., 569 p.
HUNTER, J. R., AND S. R. GOLDBERG.
1979. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.
HUNTER, J. R., AND R. LEONG.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.
HYDER, M.
1969. Histological studies on the testis of *Tilapia leucosticta* and other species of the genus *Tilapia*. Trans. Am. Microsc. Soc. 88:211-231.
INGLES, J., AND D. PAULY.
1984. An Atlas of the Growth, Mortality and Recruitment of Philippine Fishes. ICLARM, Manila, Philippines, 127 p.

JENKINS, B. W., AND J. M. GREEN.
1977. A critique of the field methodology for determining fish feeding periodicity. Environ. Biol. Fishes 1:209-214.
KAESTNER, A.
1970. Invertebrate biology. 3d ed. Intersci., N.Y., 523 p. [English translation by Levi and Levi.]
KAWAMOTO, P.
1973. Management investigation of the akule or bigeye scad (*Trachurops crumenopthalmus*). Final report to NMFS, Comm. Fish. Dev. Act PL 83-309, Project H-4-R, Hawaii Div. Fish Game, 28 p.
KLIMA, E. F.
1971. Distribution of some coastal pelagic fishes in the western Atlantic. Commer. Fish. Rev. 33(6):21-34.
KLIMA, E. F., AND D. A. WICKHAM.
1971. Attraction of coastal pelagic fishes with artificial structures. Trans. Am. Fish. Soc. 100:86-99.
LANG, W. H., AND A. ACKENHAUSEN-JOHNS.
1981. Seasonal composition of barnacle larvae (Cirripedia: Thoracica) in Rhode Island waters, 1977-78. J. Plankton Res. 3:567-575.
LEAK, J. C.
1981. Distribution and abundance of carangid larvae in the eastern Gulf of Mexico, 1971-1974. Biol. Oceanogr. 1:1-28.
MACER, C. J.
1974. The reproductive biology of the horse mackerel, *Trachurus trachurus* (L.), in the North Sea and English Channel. J. Fish Biol. 6:415-438.
1977. Some aspects of the biology of the horse mackerel, *Trachurus trachurus* (L.), in waters around Britain. J. Fish Biol. 10:51-62.
MAGNUSON, J. J., S. B. BRANDT, AND D. J. STEWART.
1981. Habitat preferences and fishery oceanography. *In* Fish behavior and its use in the capture and culture of fishes, p. 371-382. ICLARM, Manila.
MARTINEZ, S., AND E. D. HOUDE.
1975. Fecundity, sexual maturation, and spawning of scaled sardine (*Harengula jaguana* Poey). Bull. Mar. Sci. 25:35-45.
MCGURK, M.
1984. Ring deposition in the otoliths of larval Pacific herring, *Clupea harengus pallasi*. Fish. Bull., U.S. 82:113-120.
MILLER, G. C., AND W. J. RICHARDS.
1980. Reef fish habitat, faunal assemblages, and factors determining distributions in the South Atlantic Bight. Proc. Gulf Caribb. Fish. Inst., p. 114-130.
MUGIYA, Y., N. WATABE, J. M. DEAN, D. G. DUNKELBARGER, AND M. SHIMIZU.
1981. Diurnal rhythm in otolith formation in the goldfish, *Carassius auratus*. Comp. Biochem. Physiol. 68A:659-662.
MUSICK, J. A., AND J. D. MCEACHRAN.
1972. Autumn and winter occurrence of decapod crustaceans in the Chesapeake Bight, U.S.A. Crustaceana 22:190-200.
PAFFENHÖFER, G. A.
1980. Zooplankton distribution as related to summer hydrographic conditions in Onslow Bay, North Carolina. Bull. Mar. Sci. 30:819-832.
1981. Vertical zooplankton distribution on the northeastern Florida shelf and its relation to temperature and food abundance. J. Plankton Res. 5:15-33.
PANELLA, G.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* J. B. Bagenal (editor), Ageing of fish, p. 28-39. Unwin Brothers LTD, Surrey.
PERRSON, L.
1981. The effects of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) fed on fish larvae. Freshwater Biol. 11:131-138.
PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.
POLLONI, P., R. HAEDRICH, G. ROWE, AND C. H. CLIFFORD.
1979. The size-depth relationship in deep ocean animals. Int. Rev. Gesamten. Hydrobiol. 64:39-46.
POWLES, H., AND B. W. STENDER.
1976. Observations on composition, seasonality, and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. S.C. MRRI Tech. Rep. #11, 47 p.
RALSTON, S., AND G. T. MIYAMATO.
1983. Analyzing the width of daily growth increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. Fish. Bull., U.S. 81:523-535.
REEVE, M. R.
1964. Studies on the seasonal variation of the zooplankton in a marine sub-tropical inshore environment. Bull. Mar. Sci. Gulf Caribb. 14:103-122.
RICKER, W. E.
1979. Growth rates and models. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 8, p. 678-744. Acad. Press, N.Y.
ROSENBERG, A. A.
1982. Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds. Fish. Bull., U.S. 80:245-252.
SAZIMA, I.
1983. Scale eating in characoids and other fishes. Environ. Biol. Fishes 9:87-102.
SEDBERRY, G. R., AND R. F. VAN DOLAH.
1984. Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. Environ. Biol. Fishes 11:241-258.
SMITH, P. E., AND R. LASKER.
1978. Position of larval fish in an ecosystem. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:77-84.
SOKAL, R. R., AND F. J. ROHLF.
1981. Biometry. 2d ed. W. H. Freeman and Co., N.Y., 859 p.
SPURR, A. R.
1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26:31-43.
STRUHSAKER, P.
1969. Demersal fish resources: composition, distribution, and commercial potential of the continental shelf stocks off the south-eastern United States. U.S. Fish. Wildl. Serv., Fish. Ind. Res. 4:261-300.
TIEWS, K., I. A. RONQUILLO, AND P. CACES-BORJA.
1970. On the biology of the round scads (*Decapterus*) in Philippine waters. Proc. Indo-Pac. Fish. Counc. 13:82-106.
VON BERTALANFFY, L.
1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217-231.
WALLACE, R. A., AND K. SELMAN.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325-343.
WENNER, C. A.
1983. Species associations and day-night variability of trawl caught fishes from the inshore sponge-coral habitat, South Atlantic Bight. Fish. Bull., U.S. 81:532-552.
WENNER, C. A., C. A. BARANS, B. STENDER, AND F. BERRY.
1979a. Results of MARMAP otter trawl investigations in the South Atlantic Bight. I. Fall, 1973. S.C. MRRI Tech. Rep.

#33, 79 p.

1979b. Results of MARMAP otter trawl investigations in the South Atlantic Bight. II. Spring, 1974. S.C. MRRI Tech. Rep. #40, 78 p.

1979c. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III. Summer, 1974. S.C. MRRI Tech. Rep. #41, 62 p.

1979d. Results of MARMAP otter trawl investigations in the South Atlantic Bight. IV. Winter-Early Spring, 1975. S.C. MRRI Tech. Rep. #44, 59 p.

1980. Results of MARMAP otter trawl investigations in the South Atlantic Bight. V. Summer, 1975. S.C. MRRI Tech. Rep. #45, 57 p.

WENNER, E. L., D. M. KNOTT, R. F. VAN DOLAH, AND V. G. BURRELL, JR.

1983. Invertebrate communities associated with hard bottom habitats in the South Atlantic Bight. Estuarine Coastal Shelf Sci. 17:143-158.

WENNER, E. L., P. HINDE, D. M. KNOTT, AND R. F. VAN DOLAH.

1984. A temporal and spatial study of invertebrate communities associated with hard-bottom habitats in the South Atlantic Bight. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 18, 104 p.

WILK, S. J., AND M. J. SILVERMAN.

1976. Fish and hydrographic collections made by the research vessels *Dolphin* and *Delaware II* during 1968-1972 from New York to Florida. U.S. Dep. Commer., NMFS SSRF-697, 159 p.

WINDELL, J. T.

1971. Food analysis and rate of digestion. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 215-226. Blackwell Sci. Publ., Lond.

WYLLIE, M. C., E. R. HOLSTROM, AND R. K. WALLACE.

1976. Temperature preference, avoidance, shock, and swim speed studies with marine and estuarine organisms from New Jersey. Ichthy. Assoc. Brigantine, N.J. Bull. #15, 76 p.

YAMAGUCHI, Y.

1953. The fishery and biology of the Hawaiian opelu, *Decapterus pinnulatus*. M.S. Thesis, University of Hawaii, 91 p.

ZWEIFEL, J. R., AND R. LASKER.

1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

A COMPARISON OF THE AGE AND GROWTH OF THE TIGER SHARK, *GALEOCERDO CUVIERI*, FROM OFF VIRGINIA AND FROM THE NORTHWESTERN GULF OF MEXICO[1]

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ABSTRACT

Lengths at age and growth rates for the tiger shark, *Galeocerdo cuvieri*, in the northwestern Alantic and Gulf of Mexico were estimated from bands formed seasonally in the vertebral centra. The tiger shark grows rapidly compared with many other shark species. Growth rates for Gulf of Mexico juveniles were faster than for Atlantic juveniles. This produced significantly different ($P < 0.01$) estimates of the parameters of von Bertalanffy curves for the two regional samples. With sexes combined, parameter estimates for the Gulf of Mexico sample were $L_\infty = 388$ cm TL, $K = 0.184$, $t_0 = -1.13$ years; for the Atlantic sample they were $L_\infty = 440$ cm TL, $K = 0.107$, $t_0 = -2.35$ years. Males mature at approximately 310 cm TL, females at 315-320 cm TL, but the regional differences in juvenile growth rates result in different ages at maturity. In the Gulf of Mexico, males mature in 7 years, females in 8 years; in the Atlantic, males and females both mature in approximately 10 years. The largest male and female examined (381 cm TL) were 15 and 16 years of age.

The tiger shark, *Galeocerdo cuvieri*, is cosmopolitan in warm-temperate and tropical coastal and oceanic waters of the western North Atlantic (Castro 1983). It is usually found alone or in small groups of three to six individuals distributed rather homogeneously over most bottom types (Springer 1963). Because of its large size, it is one of the most frequent entries in recreational fishing tournaments, and it occurs regularly, but in low numbers, in longline catches (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981, 1986). Along the U.S. Atlantic coast, the tiger shark occurs year-round off Florida, migrates as far north as Cape Cod in summer (Casey 1964), and returns to more southerly latitudes in fall (Musick et al. 1985). In the Gulf of Mexico, the species occurs in coastal waters from spring through fall, and in deeper continental shelf and offshore regions year-round (Branstetter 1981, 1986).

The low catch rates and semisolitary nature of the tiger shark have hindered a comprehensive study of its biology. The tiger shark is both a scavenger (Gudger 1949; Clark and von Schmidt 1965) and euryphagous predator (Bass et al. 1975; Dodrill and Gilmore 1978). Information on the reproductive biology of the tiger shark must be gleaned from scattered observations on pregnant females taken in the Indo-West Pacific and Indian Ocean (Kauffman 1950; Bass et al. 1975) and in the northwestern Atlantic (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981). Age and growth rates for the tiger shark have not been reported.

Alternating opaque (calcified) and translucent (less calcified) bands form in the vertebral centra of many elasmobranchs during growth (Radtke and Cailliet 1984), and if a regular periodicity can be demonstrated for the formation of these bands throughout the life of the animal (Beamish and McFarlane 1983), they can be used to assess ages for individuals in the sample and to estimate growth rates for the population. Using these bands, age and growth data for collections of tiger sharks from Virginia and the northwestern Gulf of Mexico were developed, compared, and integrated with known life history characteristics.

METHODS AND MATERIALS

Tiger sharks were examined from research and commercial longline catches and from recreational fishing tournaments. The Atlantic sample consisted of 27 specimens taken during 1983 and 1984 summer tournaments, and 42 specimens collected in May through October on longlines fished in continental shelf waters (primarily <40 m) within a 50 km radius of the mouth of Chesapeake Bay from 1977 to 1983. The Gulf of Mexico sample consisted

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of 21 specimens taken on longlines fished in continental shelf waters of the northwestern Gulf in summer and along the shelf edge in winter from 1981 to 1985. Nine more tiger sharks were examined during a summer tournament in Texas. Between 1978 and 1985, an additional 41 specimens were tagged and released between Panama City, FL and Brownsville, TX. Data on morphometrics, lengths at maturity, and weight/length relationships were supplemented by specimens collected in the north central Gulf of Mexico (Branstetter 1981) and by 23 weight/length records from specimens taken from 1976-81 Galveston, TX shark tournaments.

Measurements were taken as the straight line distance between perpendiculars with caudal fins placed in a natural position (Dodrill 1977; Branstetter 1981, 1986). The upper caudal lobe angle was calculated to be approximately 21-22°, based on a formula by Dodrill (1977) which places the vertex of the angle at the upper caudal notch. This is slightly less than the values calculated by Thompson and Simanek (1977), who measured the angle through the center of the caudal peduncle, not the upper caudal notch. Total lengths (TL) are used throughout this report, but because measurements were taken by different people, there could have been variation in placement of the long flexible upper caudal lobe into a natural angle. Therefore, for each regional sample, regressions were calculated to compare total length to the more precisely measureable fork length (FL) or precaudal length (PCL).

Weights of tiger sharks from tournaments and Virginia specimens were made with balance beam scales, and Gulf of Mexico specimens taken on longlines were weighed with spring scales. Scales were tested for accuracy between sampling periods.

Reproductive development and maturity determinations follow Springer (1960), Clark and von Schmidt (1965), and Branstetter (1981). Males were considered mature only if the claspers were fully calcified and siphon sacs were fully developed. Sperm is produced before the claspers calcify and cannot be used as a criterion of maturity. Virginity in females, indicated by the presence or absence of a hymen covering the distal end of the oviducts, is not a criterion for maturity. Females were considered mature when developing or ripe eggs were in the ovary, eggs or embryos were present in the uteri, or by uterine expansion of nongravid females.

For age and growth analysis vertebrae were removed from 25 females (125-381 cm) and 19 males (156-381 cm) from off Virginia, and from 10 females (91-355 cm) and 7 males (140-340 cm) from the Gulf of Mexico. An additional eight Gulf of Mexico specimens (100-285 cm) had been processed for sale, and sex could not be determined. A section of the vertebral column was removed from under the origin of the first dorsal fin or, when sampling commercial operations, from the cervical region dorsal to the branchial chamber. Samples were frozen or preserved in 10% formalin and stored in ethyl or isopropal alcohol. Following methods detailed in Branstetter and McEachran (1986), individual centra were cleaned and a sagittal section cut from the center. Sections were polished on wet 400 grit sandpaper and observed with a binocular dissecting microscope using transmitted light. To block incidental light, an opaque tube was placed over the section between the microscope stage and objective.

Distinct marks (annuli), as illustrated in Casey et al. (1985: fig. 1) and Branstetter and Stiles (in press: fig. 1), were visible in the intermedialia of centrum sections. These annuli corresponded to translucent areas in the corpus calcareum and to the outer edge of translucent bands on the centrum face. The annuli formed distinct borders for the growth bands. Bands were counted without knowledge of the length of the specimen. All band counts were made by the senior author. Counts for each specimen were performed twice, and if agreement was not reached, a third count was made for comparative purposes. The distance from the section focus to each annulus, centrum dorsal radius, and marginal increment was measured on a line from the focus through the center of the intermedialia.

The periodicity of annulus formation was verified through marginal increment analysis and corroborated with comparisons to back-calculated lengths at each mark. Relative marginal increments were calculated by dividing absolute marginal increment widths by the width of the last fully formed band, and relative marginal increments were compared by month of capture. Back calculations were performed using the Dahl-Lea method (Carlander 1969) where

$$TL_i = M_i(TL)CR$$

and TL_i = total length at mark i (M_i), TL = observed length at capture, and CR = centrum radius. Back calculations were analyzed for each sample as a whole and by age class.

Tiger sharks are born in the Gulf of Mexico and along the southeastern U.S. Atlantic coast in early

summer (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981). Therefore, for simplicity, a 1 June birthday was used to estimate actual ages. For back calculations, ages were based on the age at the formation of winter annuli; therefore, for summer caught tiger sharks, there is a difference between the actual age and the age at annulus formation (i.e., a tiger shark taken in June that was aged at 6.0 years would be 5+ years of age in back calculations). To estimate growth rates, observed age/length data were applied to a computerized von Bertalanffy growth model (Fabens 1965). Males and females were taken in similar numbers, and both sexes for both samples are represented graphically; however, because of the small data base, sexes were combined for all mathematical analyses.

Apparent differences in mean lengths at age between the two samples were tested for significance using t-tests (Snedacor and Cochran 1980), and independent von Bertalanffy curves for the two regional samples were tested for differences following methods of Bernard (1981) using computer analysis (SAS Institute 1985).

RESULTS

A FL/TL plot of data from both samples (Fig. 1) can be used for general conversions of lengths reported in this paper. However, analyzed separately, the two regional samples had nonsignificantly different regression formulas for the relationships of FL or PCL to TL:

Gulf

$$FL = 0.871(TL) - 13.5 \quad (n = 33,\ r = 0.998)$$
$$PCL = 0.788(TL) - 12.1 \quad (n = 34,\ r = 0.977)$$

Atlantic

$$FL = 0.853(TL) - 10.1 \quad (n = 66,\ r = 0.994)$$
$$PCL = 0.797(TL) - 14.2 \quad (n = 68,\ r = 0.992)$$

Combining data for both samples, the relationship of centrum radii (CR) to length (TL) (Fig. 2) could be described by linear regression:

$$TL = 14.72\ CR + 51.15 \quad (n = 64,\ r = 0.972)$$

Although the regression did not pass through the origin, no correction factor, such as the Fraser-Lee method (Carlander 1969), was applied because this factor did not adequately describe the rapid embryonic growth (Casey et al. 1985; Branstetter 1986). For simplicity, this isometric relationship was used for back-calculating lengths at previous ages and did not produce Lee's phenomenon (Table 1). However, the relationship was slightly curvilinear and was more accurately described by separating the data into immature vs. mature specimens (< or > 310 cm):

$$\text{Immature - } TL = 17.7\ CR + 20.18 \quad (n = 44,\ r = 0.972)$$
$$\text{Mature - } TL = 7.6\ CR + 190.21 \quad (n = 20,\ r = 0.796).$$

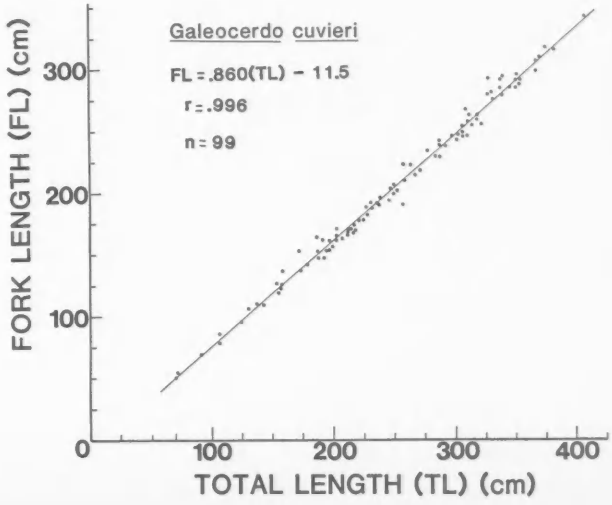

FIGURE 1.—Relationship between fork length and total length for *Galeocerdo cuvieri* taken in the Gulf of Mexico and off the Virginia coast.

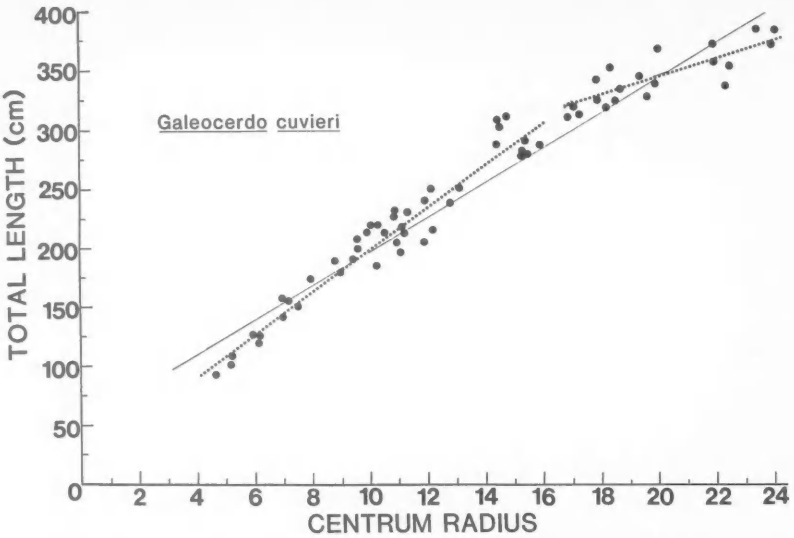

FIGURE 2.—Relationship of centrum dorsal radii to total length for *Galeocerdo cuvieri* taken in the Gulf of Mexico and off the Virginia coast. Centrum radii measurements are in ocular micrometer units (omu). 1 omu = 1.2 mm. See text for discussion of the different regressions.

Neonatal tiger sharks had only one annulus. Back calculations of length at the formation of this annulus indicated that it was formed at birth. Prebirth marks, which formed at placentation (Radtke and Cailliet 1984; Casey et al. 1985; Branstetter 1987c; Branstetter and Stiles in press), were not found in this aplacentally developing species; a condition also noted for the aplacental *Alopias vulpinus* (Cailliet et al. 1986).

Marginal increment analysis on all but neonatal tiger sharks (Fig. 3) indicated that the annuli formed in late fall or early winter (October-December) became visible off the centrum edge by January and were farthest from the centrum edge in summer. This "winter" annulus was consistent throughout the size range of the sample (Beamish and McFarlane 1983). Therefore, the first band bordered by the birth mark and the first winter annulus represented approximately 6 months growth; remaining bands formed annually.

Annuli along the periphery of centra in large (old) tiger sharks were closely spaced, making counts for these individuals more difficult. Annulus counts between the two readings were identical except for some of the larger individuals. In these cases, results of a third count matched one of the two previous counts, and this was the value accepted.

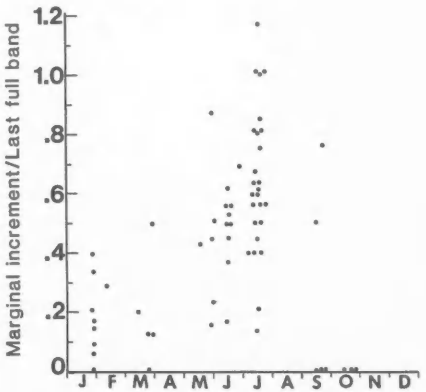

FIGURE 3.—Marginal increment widths as a ratio of the width of the last fully formed band in vertebral centra of *Galeocerdo cuvieri* compared by month. Specimens from the two regional samples are combined.

The two regional samples of tiger sharks exhibited similar growth rates. By combining observed length at age data from both samples a single von Bertalanffy curve could be fitted by using Fabens (1965)

TABLE 1.—Back calculations by age class for the Virginia and Gulf of Mexico samples of tiger sharks, *Galeocerdo cuvieri*. Ages are based on age at the formation of the winter mark. Lengths to nearest cm TL. Significantly different mean lengths at age between samples indicated by asterisks (** $P < 0.001$; * $P < 0.01$).

Winter mark	*n*	Age at the formation of the winter mark															
		B	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+
0	0	—																
1	2	76	126															
2	2	74	130	156														
3	6	73	125	159	185													
4	9	73	122	161	189	209												
5	1	84	126	160	192	219	237							ATLANTIC				
6	2	78	135	178	205	223	244	262										
7	2	75	120	151	186	218	243	259	274									
8	2	82	118	163	198	224	242	261	278	294								
9	1	73	122	148	165	196	224	249	271	290	309							
10	5	72	116	154	186	211	229	250	270	290	305	314						
11	6	72	121	159	184	211	239	262	280	300	316	326	336					
12	1	78	118	144	176	211	230	245	270	284	296	311	322	330				
13	1	73	128	183	219	238	256	284	302	317	326	335	348	356	366			
14	1	62	107	153	187	207	253	270	281	299	314	324	337	345	351	362		
15	2	77	123	158	189	214	236	261	287	301	313	325	334	346	355	364	372	
16	1	72	111	150	180	198	214	244	260	274	285	304	318	331	346	359	364	378
$\bar{X}$		74	122	159**	188**	213**	237**	258**	277**	295*	310*	321	334	342	355	362	369	378
cm/yr		[1](48)	37	29	25	24	21	19	18	15	11	13	8	13	7	7	9	
cm/yr		[1](49)	51	35	29	24	18	18	17	16	13	9						
$\bar{X}$		73	122	173**	208**	237**	261**	279**	297**	314*	330*	343	352					
0	1	77																
1	4	70	114															
2	3	74	129	169														
3	5	74	125	180	212													
4	2	80	124	170	214	241												
5	2	77	125	169	208	235	267											
6	1	68	115	166	198	227	256	281										
7	2	74	130	172	197	233	249	274	288									
8	1	61	105	179	202	229	250	275	300	307								
9	2	74	126	178	209	237	263	280	301	317	329							
10	0	—	—	—	—	—	—	—	—	—	—	—						
11	1	68	113	166	215	254	283	290	306	316	333	343	352					

[1]Six months growth.

procedure (Fig. 4) to adequately describe the growth rate. However, young age classes in the Gulf of Mexico (hereafter referred as Gulf) sample were slightly larger at age than their Atlantic counterpart. Independent von Bertalanffy curves for each data set had different parameter estimates. Regressions of the curves, linearized by log transformation, were analyzed for covariance (SAS Institute 1985) and were significantly different ($P < 0.0001$). Simultaneous nonlinear regression analysis of the two von Bertalanffy curves derived from back-calculated mean lengths at age produced parameter estimates with nonoverlapping simultaneous confidence intervals (Bernard 1981).

Back calculations by age class for each sample (Table 1) also showed the more rapid growth of the Gulf juveniles. Mean lengths at the formation of the winter annuli were significantly different ($P < 0.01$ or $P < 0.001$) for early age classes of the two samples. Neonates in both samples increased nearly 50 cm in length the first 6 months, and the Age I Gulf tiger sharks continued to grow at 50 cm/year, but Atlantic Age I individuals grew <40 cm/year. Gulf tiger sharks continued to grow approximately 4 cm/year faster than the Atlantic population until the fourth year. Growth rates then became similar; Gulf tiger sharks were simply larger at age.

Observed and back-calculated lengths at age (Table 2) corresponded within each sample. Comparisons of observed and back-calculated lengths did not indicate the occurrence of Lee's phenomenon. Differences in observed and back-calculated lengths at age were attributable to the fact that most specimens in both samples were taken in summer; therefore, observed lengths at age were larger than back-calculated lengths at age based on the winter formed annuli.

The growth rate estimated from centra was validated with one tag-recapture. A female, tagged 3 November 1978, was estimated to be 230 cm, and

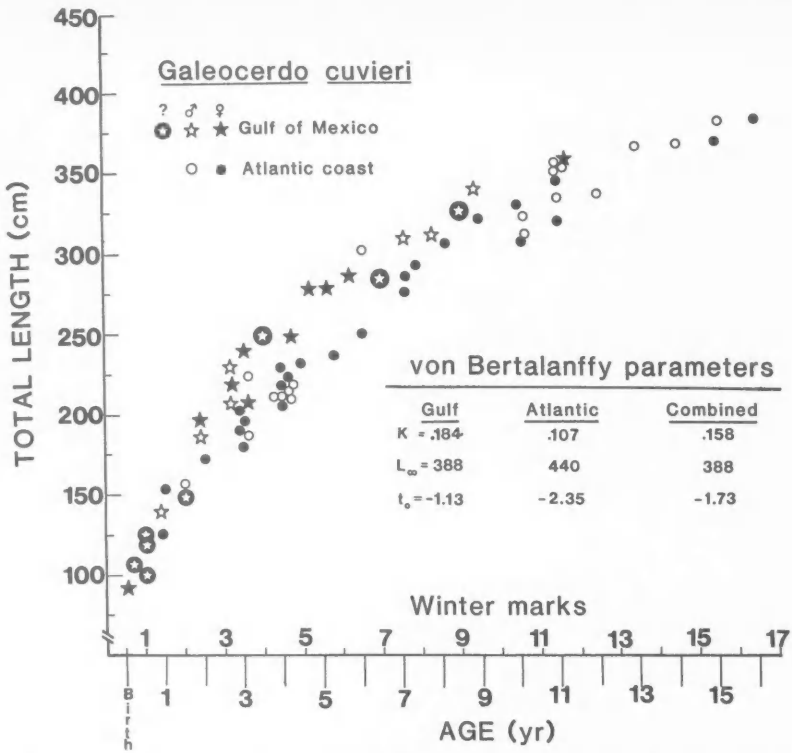

FIGURE 4.—Length at age for *Galeocerdo cuvieri* from the Gulf of Mexico and the Atlantic coast of Virginia. Individuals are plotted by their estimated actual ages (time elapsed since formation of the last winter mark). Birthdays set at 1 June.

at recapture, 7 April 1984, was estimated to be 320 cm from the weight/length relationship. The tiger shark grew 90 cm in 5.4 years. By using the age/length relationship estimated by the growth curve (Fig. 4), the shark would have been 3.4 years of age when tagged and 8.8 years of age at recapture.

Even with the relatively rapid growth rate exhibited by this species, a length-frequency analysis for both samples (Fig. 5) did not distinguish age classes. The size distribution did indicate that young juvenile tiger sharks occur only rarely in the Virginia region.

Males matured at approximately 310 cm, females at 315-320 cm, and the differences in growth rates between the two samples meant that they reached maturity at different ages. For the Gulf of Mexico, the smallest mature males (310, 311 cm) were 8.0 and 7.8 years old. The largest male aged (340 cm) was only 8.8 years old. Back calculations indicated that this individual grew relatively rapidly compared with smaller individuals in the sample, and the only larger male collected (363 cm) was not aged. The smallest mature female (325 cm) was 8.8 years old, the largest (355 cm) was 11.2 years old. For the Atlantic sample, two immature males (310, 311 cm) were not aged, but a 312 cm mature male was 10.1 years old. The largest male (381 cm) was 15.1 years old. The largest immature female (307 cm) was 8.1 years of age, the smallest mature females (318, 319 cm) were 9.0 and 11.1 years of age, and the largest female (381 cm) was 16.1 years old.

The rapid linear growth early in life did not correspond to a great increase in the weight of the individuals (Fig. 6). Growth from the third through the seventh winter decreased from 30 to 20 cm/year, and weights increased during this period. As the

TABLE 2.—Comparison of length at age for observed and back-calculated data for Atlantic and Gulf populations of the tiger shark, *Galeocerdo cuvieri*. Lengths are to the nearest cm TL. Values indicate low-mean-high (*n*) for each age class.

Winter mark:	0	I	II	III	IV	V
Age:	0	0+	1+	2+	3+	4+
Gulf						
observed	91-99-106 (2)	100-121-140 (4)	150-179-199 (3)	205-220-240 (5)	248-249-250 (2)	278-279-279 (2)
back calculation	50-73-85 (25)	96-122-137 (23)	149-173-184 (19)	192-208-228 (16)	225-237-254 (11)	239-261-283 (9)
Atlantic						
observed	NA (0)	125-140-155 (2)	156-165-173 (2)	180-192-225 (6)	205-216-229 (9)	237 (1)
back calculation	60-74-84 (44)	101-122-149 (44)	138-159-188 (42)	161-188-220 (40)	183-213-238 (34)	202-237-256 (25)

Winter mark:	VI	VII	VIII	IX	X	XI
Age:	5+	6+	7+	8+	9+	10+
Gulf						
observed	288 (1)	285-298-310 (2)	311 (1)	325-333-340 (2)	NA (0)	355 (1)
back calculation	272-279-290 (7)	283-297-306 (6)	307-314-318 (4)	325-330-333 (3)	343 (1)	352 (1)
Atlantic						
observed	250-276-302 (2)	278-282-286 (2)	292-300-307 (2)	318 (1)	307-322-335 (5)	319-341-354 (6)
back calculation	221-258-284 (24)	245-277-302 (22)	270-295-317 (20)	292-310-327 (18)	304-321-341 (17)	315-334-349 (12)

Winter mark:	XII	XIII	XIV	XV	XVI
Age:	11+	12+	13+	14+	15+
Atlantic					
observed	338 (1)	368 (1)	368 (1)	370-376-381 (2)	381 (1)
back calculation	340-343-356 (6)	346-355-366 (5)	359-362-369 (4)	364-369-378 (3)	378 (1)

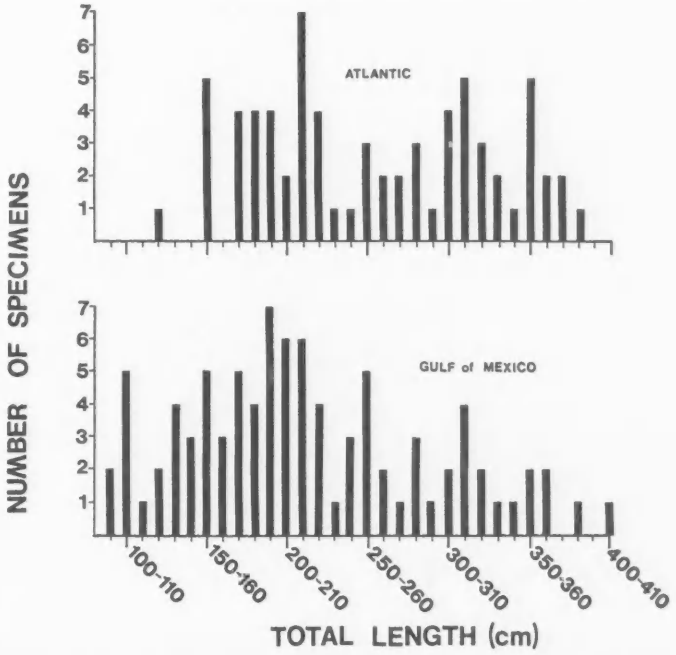

FIGURE 5.—Length frequency of *Galeocerdo cuvieri* collected off Virginia and in the Gulf of Mexico. Specimens are grouped into 10 cm size classes.

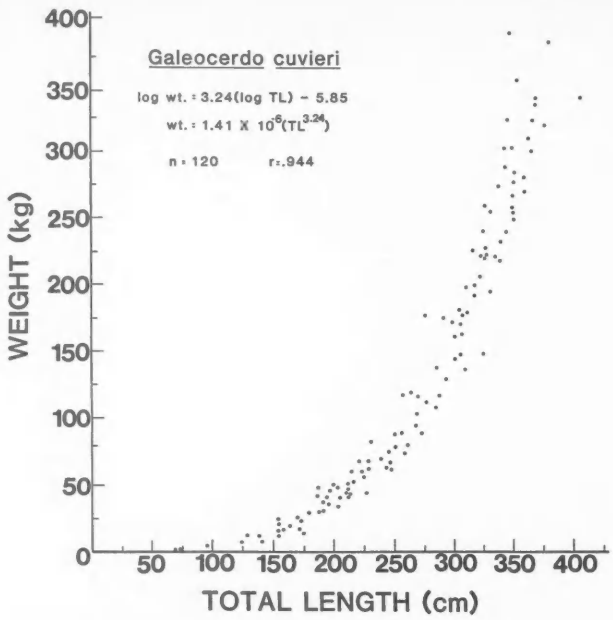

FIGURE 6.—Weight/length relationship for Atlantic and Gulf of Mexico *Galeocerdo cuvieri*, sexes combined.

animals matured at 310-320 cm, linear growth slowed from 15 cm/year to <10 cm/year, and weights increased dramatically.

DISCUSSION

An isometric relationship between centrum growth and length has been noted for many shark genera (Cailliet et al. 1983; Gruber and Stout 1983; Branstetter and McEachran 1986). The slight curvilinear relationship between centrum growth and length noted for *Galeocerdo cuvieri* suggested there were two distinct growth stanzas. A similar relationship was also noted for *Isurus oxyrinchus* (Pratt and Casey 1983). The point of inflection in the curve is generally at the length corresponding to the onset of maturity, a decreased linear growth rate and an increased weight gain rate. Apparently, centrum growth is correlated to the structural support necessary for length increases, but an increasing rate of weight gain does not require additional strengthening of the vertebral column.

Marginal increment analysis of annulus periodicity demonstrated that one growth band, consisting of one calcified opaque zone and one less calcified translucent zone, formed annually. A similar periodicity for growth bands or annuli has been verified for several shark genera (Gruber and Stout 1983; Cailliet et al. 1986; Branstetter and McEachran 1986) and validated using tetracycline injected *Negaprion brevirostris* (Gruber and Stout 1983), *Triakis semifasciatus* (Smith 1984), *Rhizoprionodon terraenovae*, and *Carcharhinus plumbeus* (Branstetter 1987a). In contrast, Parker and Stott (1965) and Pratt and Casey (1983) provided evidence that lamnoids produce two band pairs per year, and Natanson (1984) could find no regular periodicity in centrum bands of *Squatina californica*.

Our estimates indicated the tiger shark doubles in length the first year of life. This is supported by growth of a full-term embryo (69 cm) placed in an aquarium by Clark and von Schmidt (1965) on 21 May, where it survived 12 weeks growing to 89 cm.

Rapid linear growth for juvenile tiger sharks may be necessary for adequate cohort survival. With a 13-16 mo gestation period (Clark and von Schmidt 1965) and a mating season which occurs before full-term females have pupped, the female reproductive

cycle is at least 2 years. Considering the litter size (40-70 pups) (Kauffman 1950; Bass et al. 1975; Branstetter 1981), natural mortality must be high for young age classes. Pups are born in coastal waters at a relatively large size (>70 cm) which reduces some predation, but the elongate, flexible body produces an inefficient anguilliform swimming motion. Additionally, early in life, the caudal fin is extremely flexible and has a low thrust angle (Thompson and Simanek 1977). The combination of these characteristics precludes rapid swimming speeds, thus making the pups vulnerable to predation by the abundant coastal sharks including their own species. Not only does rapid linear growth make them larger than most potential predators, it may help decrease predation by increasing swimming efficiency and speed through increased body rigidity (producing a more carangiform motion) and increased caudal fin thrust angle.

Linear growth continues at >20 cm/year until the tiger sharks are near maturity. Such rapid growth is similar to that noted for several lamnoids (Parker and Stott 1965; Gruber and Compagno 1981; Pratt and Casey 1983; Cailliet et al. 1985), but contrasts sharply to the slow growth rates estimated for several carcharhinids and sphyrnids (Thorson and Lacy 1982; Gruber and Stout 1983; Schwartz 1983a). Even the more rapidly growing carcharhinids do not have such large relative increases in length (Parsons 1985; Branstetter and McEachran 1986).

The mean lengths at age between the Gulf of Mexico and Atlantic tiger sharks were significantly different, and probably represent ecophenotypic differences between the two regions. However, the two regional groups are not isolated. Our one tag-recapture was tagged off Mobile Bay, AL and recaptured in the Florida Straits off Havana, Cuba, and there are similar tag returns of tiger sharks that moved between the Gulf of Mexico and the Atlantic (J. Casey pers. commun.[4]). However, long migrations between the two regions may be restricted to larger individuals with juveniles remaining in their respective regions.

If juvenile tiger sharks do remain in their respective regions early in life, growth rate differences between the two regions may be caused by differences in early life histories. In the Gulf of Mexico, the pups apparently only migrate short distances inshore-offshore seasonally. In the Atlantic, the pups are born south of Cape Hatteras, probably in the Florida region (Dodrill 1977). These neonates may not migrate north during their first year, as small individuals, <150 cm, are rare in the Virginia region (Fig. 5). During this time, the growth rates for both groups are similar. The extensive northern migration for 1+ year old Atlantic juveniles, 150-200 cm, may be energetically costly, hindering growth. Therefore, the Gulf young that do not migrate great distances are able to attain greater lengths during this time period. The increased swimming efficiency attained with lengths >250 cm could possibly explain why growth rates become similar.

For juveniles of both regions, the energy requirements for the inefficient swimming motion and rapid linear growth apparently restrict any great increase in weight (Fig. 6). Only after the tiger sharks reach lengths >200 cm (3+ years of age) does weight increase substantially, and correspondingly linear growth begins declining. After reaching maturity (310-320 cm) linear growth is <10 cm/year while weight growth is substantial, corresponding to the change in centrum radius/length relationship (Fig. 3).

The von Bertalanffy parameter estimates for the two collections closely bracket known life history characteristics. With sexes combined, the L_∞ for the Gulf of Mexico collection and for both samples combined (388 cm) is smaller than many reported large individuals, but is a reasonable compromise between the maximum reported lengths for males and females: 419 cm individual (McCormick et al. 1964); 370 cm male, 410 cm female (Bass et al. 1975); 410 cm female (Branstetter 1981); and a 381 cm male and female from this study. However, the tiger shark is thought to attain lengths in excess of 450 cm (Bigelow and Schroeder 1948; Castro 1983), more in agreement with the L_∞ for the Atlantic sample (440 cm). The t_0 value for the Gulf sample (−1.13 years) is accurate, but the 13-16 mo gestation period is overestimated for the Atlantic sample (−2.35 years). The t_0 value for many shark species overestimates the gestation period (Casey et al. 1985; Branstetter 1986). The K values for each analysis reflect the rapid growth rate of this species and are similar to some of the more rapidly growing *Carcharhinus* species such as *C. limbatus*, *C. brevipinna* (Branstetter 1987c), *C. falciformis* (Branstetter 1987b), and *C. acronotus* (Schwartz 1983b).

At the estimated growth rate for the largest individuals (5-10 cm/year), exceptionally large specimens, 400-450 cm, would be 20-25 years of age. The

[4]J. Casey, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882, pers. commun. June 1986.

von Bertalanffy curve using observed lengths at age produced an estimated age at L_∞ for the Gulf sample of 28 years, and 37 years for the Atlantic sample. This would mean that the species matures at 30-50% of its maximum age, and with a reproductive cycle of greater than 2 years, a female would reproduce less than 10 times. On the other hand, von Bertalanffy curves derived using back-calculated lengths at age for both samples produced estimated ages at L_∞ of 45-50 years. Exceptionally high ages at L_∞ may be due to the exponential function of the model, or it is also possible that as tiger sharks attain sizes near their maximum weight or length, centrum growth and band formation do not accurately represent age. Because no exceptionally large individuals were aged, we are unable to determine which is the case. Even so, the data indicate that the tiger shark is long-lived with a relatively low fecundity, and natural mortality for the young may be high. As with many other elasmobranchs, this combination of *K*-selected characteristics may result in an overexploitation of this species under increased recreational and commercial fishing pressure (Musick and Colvocoresses 1986).

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LITERATURE CITED

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy.
1975. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Carcharhinus* and *Mustelus*) and Sphyrnidae. Oceanogr. Res. Int. (Durban) Invest. Rep. 38, 100 p.

Beamish, R. J., and G. A. McFarlane.
1983. The forgotton requirements for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735-743.

Bernard, D. R.
1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquat. Sci. 38:233-236.

Bicelow, H. B., and W. C. Schroeder.
1948. Sharks. *In* Fishes of the Western North Atlantic. Part I, No. 1, p. 59-546. Mem. Sears Found. Mar. Res., Yale University.

Branstetter, S.
1981. Biological notes on the sharks of the north central Gulf of Mexico. Contrib. Mar. Sci. 24:213-34.
1986. Biological parameters of the sharks of the northwestern Gulf of Mexico in relation to their potential as a commercial fishery resource. Unpubl. Ph.D. Thesis, Texas A&M University, 138 p.
1987a. Age and growth validation of new born sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia 1987:293-300.
1987b. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. Environ. Biol. Fishes 19:161-174.
1987c. Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. Copeia 1987.

Branstetter, S., and J. D. McEachran.
1986. Age and growth of four carcharhinid sharks common to the Gulf of Mexico: a summary paper. *In* T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (editors), Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes, p. 361-371. Ichthol. Soc. Jpn., Tokyo.

Branstetter, S., and R. Stiles.
In press. Age and growth estimates for the bull shark, *Carcharhinus leucas*, in the northern Gulf of Mexico. Environ. Biol. Fishes.

Cailliet, G. M., L. K. Martin, J. T. Harvey, D. Kusher, and B. A. Welden.
1983. Preliminary studies on the age and growth of the blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. *In* E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, p. 179-188. U.S. Dep. Commer. NOAA Tech. Rep. NMFS 8.

Cailliet, G. M., L. J. Natanson, B. A. Welden, and D. Ebert.
1985. Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. South. Calif. Acad. Sci. Mems. 9:49-60.

Cailliet, G. M., R. L. Radtke, and B. A. Welden.
1986. Elasmobranch age determination and verification: a review. *In* T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (editors), Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes, p. 345-360. Ichthol. Soc. Jpn., Tokyo.

CARLANDER, K. D.
1969. Handbook of freshwater fishery biology. Volume 1. Iowa St. Univ. Press, Ames, 752 p.

CASEY, J. G.
1964. Angler's guide to the sharks of the northeastern United States, Maine to Chesapeake Bay. U.S. Fish Wildl. Serv. Circ. 179, 32 p.

CASEY, J. G., H. L. PRATT, JR., AND C. E. STILLWELL.
1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 42:963-975.

CASTRO, J. I.
1983. The sharks of North American waters. Texas A&M Univ. Press, College Station, 180 p.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15:13-83.

DODRILL, J. W.
1977. A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. Unpubl. MS Thesis, Fla. Inst. Tech., 304 p.

DODRILL, J. W., AND R. G. GILMORE.
1978. Land birds in the stomachs of tiger sharks, *Galeocerdo cuvieri* (Peron and Lesueur). Auk 95:585-586.

FABENS, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.

GRUBER, S. H., AND L. J. V. COMPAGNO.
1981. Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus*. Fish. Bull., U.S. 79:617-640.

GRUBER, S. H.,, AND R. G. STOUT.
1983. Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). *In* E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, p. 193-205. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

GUDGER, E. W.
1949. Natural history notes on tiger sharks, *Galeocerdo tigrinis*, caught at Key West, Florida, with emphasis on food and feeding habits. Copeia 1949:39-47.

KAUFFMAN, D. E.
1950. Notes on the biology of the tiger shark (*Galeocerdo articus*) from Philippine waters. U.S. Fish Wildl. Serv. Res. Rep. 16, 10 p.

MCCORMICK, H. W., T. ALLEN, AND W. YOUNG.
1963. Sharks on a line. *In* Shadows in the sea - the sharks, skates, and rays, Chap. 4, p. 89-114. Weathervane Books, N.Y.

MUSICK, J. A., AND J. A. COLVOCORESSES.
In press. Seasonal recruitment of subtropical sharks in Chesapeake Bight USA. *In* A. Yanez-Anancibia and D. Pauly (editors), Proceedings of a workshop in tropical coastal demersal communities. Carman, Campeche, Mexico, 1986.

MUSICK, J. A., J. A. COLVOCORESSES, E. F. LAWLER, AND W. G. RASCHI.
1985. Distribution of sharks in Chesapeake Bight. [Abstr.] Proceedings of the 65th Annual Meeting of the American Society of Ichthyologists and Herpetologists.

NATANSON, L. J.
1984. Aspects of the age, growth, and reproduction of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. Unpubl. MA Thesis, San Jose St. Univ., San Jose, CA 71 p.

PARKER, H. W., AND F. C. STOTT.
1965. Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). Zool. Meded. 40: 305-319.

PARSONS, G. R.
1985. Growth and age estimation of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*: a comparison of techniques. Copeia 1985:80-85.

PRATT, H. L., JR., AND J. G. CASEY.
1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can. J. Fish. Aquat. Sci. 40:1944-1957.

RADTKE, R. L., AND G. M. CAILLIET.
1984. Age estimation and growth of the gray reef shark, *Carcharhinus amblyrhynchos*, from the northwestern Hawaiian Islands. *In* Proceedings Second Symposium on Resource Investigations of the Northwestern Hawaiian Islands, p. 121-127. UNI-SEAGRANT-MR-84-01.

SAS INSTITUTE, INC.
1985. SAS User's Guide: Basics, SAS User's Guide: Statistics, SAS/Graph Software Version 5. SAS Institute Inc., Cary, NC.

SCHWARTZ, F. J.
1983a. Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrna lewini*, and dusky, *Carcharhinus obscurus*, sharks based on vertebral ring counts. *In* E. D. Prince and L. M. Pulos (editors, Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, p. 167-174. U.S. Dep. Commer. NOAA Tech. Rep. NMFS 8.
1983b. Occurrence, abundance, and biology of the blacknose shark, *Carcharhinus acronotus*, in North Carolina. Northeast Gulf Sci. 7:29-47.

SMITH, S. E.
1984. Timing of vertebral-band deposition in tetracycline injected leopard sharks. Trans. Am. Fish. Soc. 113:308-313.

SNEDACOR, G. W., AND W. G. COCHRAN.
1980. Statistical methods. Iowa State Univ. Press, Ames, 507 p.

SPRINGER, S.
1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv. Fish. Bull. 61:1-38.
1963. Field observations on large sharks of the Florida-Caribbean region. *In* P. W. Gilbert (editor), Sharks and survival, Sect. II. Ch. 3, p. 95-113. Heath and Co., Boston.

THOMPSON, K. S., AND D. E. SIMANEK.
1977. Body form and locomotion in sharks. Am. Zool. 17: 343-354.

THORSON, T. B., AND E. J. LACY, JR.
1982. Age, growth rate and longevity of *Carcharhinus leucas* estimatod from tagging and vertebral rings. Copeia 1982: 110-116.

ECOLOGICAL CONSEQUENCES OF MECHANICAL HARVESTING OF CLAMS

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ABSTRACT

A field experiment was performed in 1,225 m^2 plots in each of two shallow estuarine habitats, a seagrass bed and a sand flat, in Back Sound, North Carolina (USA), to test the impact of clam raking and two different intensities of mechanical harvesting of clams ("clam kicking") for up to 4 years on 1) hard clam, *Mercenaria mercenaria*, recruitment, 2) seagrass biomass, 3) the density of benthic macroinvertebrates, and 4) the density of bay scallops, *Argopecten irradians*. The removal of adult hard clams with the contingent sediment disturbance had ambiguous effects on the recruitment of hard clams: in the sand flat recruitment tended to be lower (but not significantly) in intense-clam-kicking matrices than in controls, whereas in seagrass recruitment of hard clams did not not show a clear response to treatment. In the raking and light-clam-kicking matrices, seagrass biomass fell immediately by ≅25% below controls but full recovery occurred within a year. In the intense-clam-kicking matrices, seagrass biomass fell by ≅65% below levels expected from controls; recovery did not begin until more than 2 years passed, and seagrass biomass was still ≅35% lower than predicted from controls 4 years later. Clam harvest did not affect either the density or species composition of small benthic macroinvertebrates from sediment cores, probably because of their rapid capacity for recolonization and generally short life spans. In all treatments, densities of benthic macroinvertebrates (mostly polychaetes) were substantially higher in the seagrass than in the sand flat during October samplings but equal during March samplings. Bay scallop density declined with declining seagrass biomass across harvest treatments, but the intense-clam-kicking matrices contained even fewer bay scallops than their seagrass biomass would predict, perhaps because of enhanced patchiness of the remaining seagrass.

The relative inertia of the change in seagrass biomass following extensive destruction in the intensely kicked matrices suggests that seagrass replanting may be an extremely important means of returning disturbed, unvegetated areas to seagrass systems. Emergence during summer of a between-habitat gradient in infaunal densities (higher in seagrass than in sand) supports the hypothesis that seagrass provides a partial prey refuge for infaunal invertebrates. The failure of the benthic macroinvertebrate density to respond to clam harvest treatments in both sand flats and seagrass beds implies that the polychaetes which dominate recover rapidly from disturbance and are probably not adversely affected by clam harvest. The negative and long-lasting impact of intense hard clam harvest on seagrass biomass with its effects on other fisheries, including bay scallops, implies that hard clam fisheries should be managed to minimize the intensity of harvest within seagrass beds.

Technological innovation is frequently accompanied by an increased risk of harm to various aspects of the natural environment (e.g., Dickie 1974). While such innovation can be considered economically desirable and even inevitable, environmental managers still require ecological inputs to enable them to reach properly informed compromises between uncontrolled application of new technology and unnecessarily cautious protection of natural ecosystems. Because of its inherent lack of general principles and paradigms, ecology is rarely able to provide immediate answers to practical questions of the probable impact of new technology. Consequently, careful studies of the ecological impact of the application of each specific new technology are often necessary. Such studies can not only provide necessary applied information but also contribute to a better basic understanding of the specific system that is being explored.

Although fisheries biologists are renowned for managing harvests in a way that will sustain a maximum yield or maximize yield per recruit (Ricker 1975), studies are only occasionally undertaken to compare the environmental damage caused by alternative fishing gears and technologies (e.g., Caddy 1973; Peterson et al. 1983a). Such studies are most common in estuarine and other shallow-water fisheries, where high coastal productivity of diverse stocks induces intensive exploitation of a common area by multiple, potentially interfering fisheries. As technological advances in fishing gear have been made, this potential for interfishery competition has grown, as has the need for understanding the envi-

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ronmental consequences of the utilization of new, alternative technologies.

Fisheries for the hard clam, *Mercenaria mercenaria* (L.), and other sedentary benthic invertebrates require the use of either hand implements (rakes, hoes, etc.) or boat-drawn gear (dredges, trawls, etc.). Managers of benthic invertebrate fisheries may turn to the subdiscipline of benthic ecology to seek predictions of the relative environmental and ecological consequences of utilizing various alternative fishing gears or of permitting technologically new substitutions for traditional fishing methodologies. Unfortunately, benthic ecologists are frequently unable to provide confident answers to many questions, often either because the fisheries applications involve a far larger scale than can be or has been practically accommodated in basic experimental research designs or because the questions fall into an area of current debate and ongoing study in the basic science of the field.

One might take, as an example of the poor predictive capacity of benthic ecology, the question of whether widespread adoption of mechanical harvesters by commercial *M. mercenaria* fishermen will affect the future recruitment success of *M. mercenaria* in the local area of harvest. Most fisheries biologists agree that the mechanical harvesters are more efficient in gathering hard clams from a given area and cause more physical disruption of the bottom than the alternative hand methods of raking and tonging. Even given these assumed differences, benthic ecology provides mixed and conflicting predictions of the impact of switching to mechanical harvesters. Basic studies of adult-larval interactions, including some among suspension-feeding bivalves (Woodin 1976; Williams 1980; Peterson 1982b), might suggest that removal of large, adult suspension feeders would enhance the survivorship of settling larvae and thereby increase the recruitment success of *M. mercenaria* in the efficiently harvested areas. Yet, the experimental results on which such a prediction is based were achieved on a much smaller spatial scale and probably depend upon absolute density (or feeding rate) of all suspension feeders in an unspecified way. It is conceivable that the virtual removal of *M. mercenaria* over a substantial area might remove an important settlement cue (produced by adults) needed for larval habitat selection (e.g., Meadows and Campbell 1972; Gray 1974). If this were true, recruitment success of *M. mercenaria* would decline with the intensity of harvest. Similarly, benthic ecology provides conflicting predictions about the effects of the increased physical disburbance of mechanical harvesting on recruitment success of *M. mercenaria*. On the one hand, *M. mercenaria* recruits might be expected to suffer increased mortality from burial during massive sediment disturbance (Rhoads 1974; Myers 1977; Thistle 1981; Wilson 1981). Yet, larvae of many species settle more densely into disturbed bottoms (Gray 1974; McCall 1977; Hulberg and Oliver 1980). Again, these signals are conflicting but, even more importantly, experimental benthic ecology is unable to predict adequately whether the scale and intensity of disturbance during commercial clam harvesting are appropriate to invoke either of these processes.

Because of the restricted scale of past field experiments and the consequent limitations of benthic ecology in the applied arena, we designed controlled field experiments to test the impact of mechanical clam harvesting on a large scale, sufficient to provide environmental data to resource managers and to extend simultaneously the scope of basic experimental, benthic ecology. Specifically, we tested on a 1,225 m^2 scale whether the harvest of *M. mercenaria*, with its attendant physical disruption of the bottom, affected the 1) recruitment success of *M. mercenaria*, 2) biomass of seagrasses, 3) density of bay scallops, and 4) density of all other benthic macroinvertebrates. We tested these harvest effects in each of two common estuarine habitats, a sand flat and a seagrass bed, and followed not only the immediate response to harvesting but also the changes in most variables over a subsequent 3.5-yr period. Thus, the need for ecological data to use in fisheries management provided an opportunity to expand the temporal and spatial scale of experiments in marine benthic ecology and thereby evaluate our ability to extrapolate from previous theory based on smaller scales.

METHODS

To test whether the type and/or intensity of hard clam, *Mercenaria mercenaria* (L.), harvest has any detectable effect on 1) its own recruitment, 2) seagrass biomass, 3) bay scallop, *Argopecten irradians*, density, or 4) density of small benthic macroinvertebrates, we performed a large-scale field experiment at sites along the southern (barrier island) margin of Back Sound near Beaufort, NC (Fig. 1). This experiment was conducted in a seagrass meadow and in an unvegetated sand flat approximately 500 m to the west to permit a test of whether effects of harvest vary with habitat. This general area and its physical characteristics are described in several previous publications (Sutherland and Karlson 1977; Nelson 1979; Peterson et al. 1983b, 1984). Back

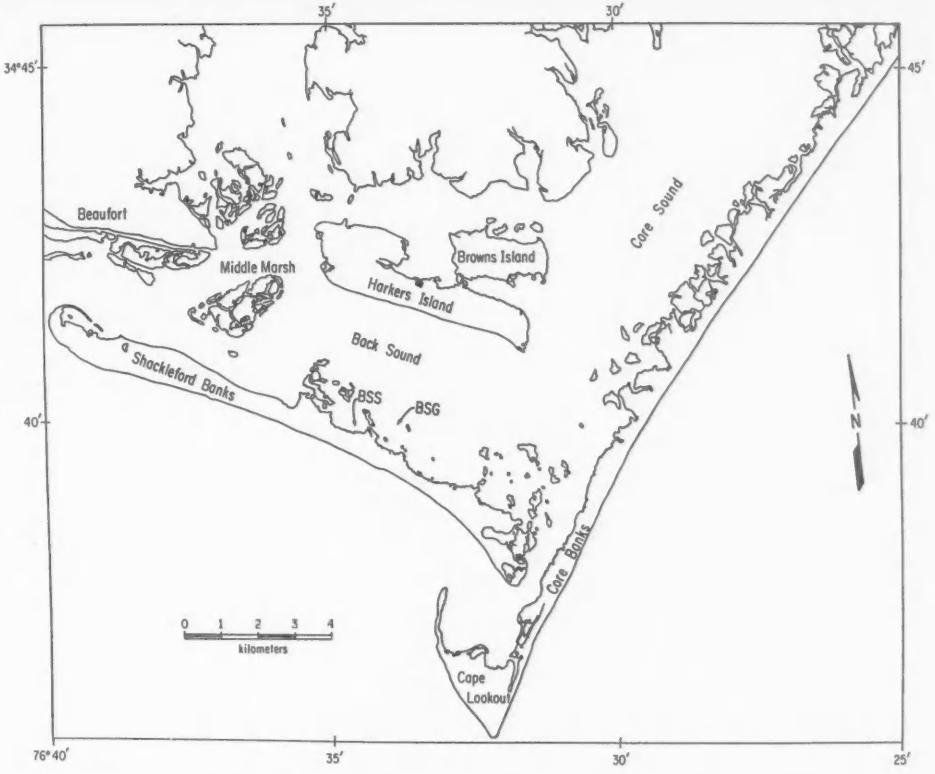

FIGURE 1.—The locations of the study sites in eastern North Carolina, near Cape Lookout. BSS indicates the sand-flat and BSG the seagrass-bed locations. Tick marks on the margins of the figure denote minutes of N. latitude and W. longitude.

Sound is a shallow marine lagoon with a lunar tide of about 0.6 m range, little salinity variation (28-34‰), and a wide seasonal temperature range from a winter monthly minimum of 2°-4°C to a summer monthly maximum of 29°-30°C. In January 1980, we selected in each habitat 6 square plots (matrices) of 1,225 m^2 area, each of which had a virtually constant water depth of about 0.1-0.3 m at low tide and homogeneous surface appearance. Specifically, all seagrass matrices held a spatially uniform cover of a seasonally varying mixture of two seagrasses, eelgrass *Zostera marina* and shoalgrass *Halodule wrightii*, whereas no sand-flat matrix contained seagrasses. These seagrass matrices had been continuously vegetated from at least 1974 until 1980 and the seagrass cover had not extended over the sand flat during that same period (Peterson et al. 1984).

Before harvest treatment, we subsampled all 6 matrices in each habitat to test whether there were any initial differences among matrices in response variables. This sampling occurred between 22 February and 31 March 1980 in the sand flat and from 1 April to 6 May 1980 in the seagrass bed. A fixed number (9 or 36) of uniformly distributed 0.25 m^2 subsamples was taken from each matrix to estimate abundance of hard clams, bay scallops, and seagrass (Table 1). A uniform sampling array was chosen to reduce the field effort and to avoid risk of sampling at or even near (<1 m) the same locations during subsequent sampling. A grid of marked ropes attached to equally spaced stakes was placed around the circumference of each matrix and moved to a new, randomly chosen set of positions for each new sampling date, thus producing a "frame shift" of the sampling template.

TABLE 1.—Temporal design of data collections and of experimental treatments for both habitats, 1980-84. Entries are numbers of samples[1] taken per matrix.

Parameter estimated	Spring 1980 22 Feb.- 6 May	Harvest treatment 12-30 May	Fall 1980 20 Oct.- 10 Nov.	Harvest treatment 19 Dec.- 22 Feb.	Spring 1981 2-13 Mar.	Fall 1981 4 Oct.- 3 Nov.	Fall 1982[2] 20-29 Oct.	Fall 1983[2] 28-31 Oct.	Fall 1984[2] 22-29 Oct.
Total hard clam density	36		36		9	36	9	9	0
Density of hard clam recruits	36		36		9	36	9	9	0
Seagrass dry mass	36		36		9	36	9	9	9
Bay scallop density	0		36		9	36	9	9	0
Density of benthic macro-invertebrates	6		6		6	6	0	0	0
Sediment size distribution parameters	3		0		0	0	0	0	0

[1]In all cases where 36 or 9 samples were taken per matrix, these were ¼ m^2 samples distributed uniformly across the matrix such that no sample fell within 1 m of any previous sample location. Where 6 or 3 samples were taken, these were chosen at random from a group of 9 uniformly distributed samples positioned in a similar way to avoid any overlaps. All sediment samples were cores of 5 cm diameter × 20 cm deep. Macroinvertebrate samples were cores of 10 cm diameter × 25 cm deep.

[2]Data taken from only the seagrass habitat on these dates.

To collect a repeatable sample, we first inserted a 0.25 m^2 circular metal sampling frame penetrating to a depth of 15 cm and used an hydraulic suction dredge to excavate the complete contents to that same depth. The material was collected in a 3 mm nylon mesh bag (for description and sampling efficiency, see Peterson et al. 1983b). All living *M. mercenaria* and *A. irradians* were removed from the mesh bag and placed in separate, labeled plastic bags for return to the laboratory. For all *M. mercenaria* we measured length in the longest anteroposterior dimension, and for all *A. irradians* we measured the distance from the flat top of the hinge to the ventral margin using vernier calipers. Seagrass material from the mesh bag was packaged in marked plastic bags in the field and returned to the laboratory, where it was gently rinsed in freshwater to remove attached salt and sediments, and dried to constant weight (2-4 days) at 105°C.

To estimate densities of small benthic macroinvertebrates, we took 9 uniformly distributed samples from each matrix in each habitat on 4 sampling dates (Table 1). We processed and analyzed a randomly chosen subset of 6 of these 9 samples for each matrix. The strategy of taking more samples than one expects to analyze is optimal when marginal costs of additional sampling are low, because extra replicates are then available for later analysis if among-sample variation proves so unexpectedly high as to reduce statistical power to an unacceptable level. Benthic invertebrates were collected using 10 cm diameter cores taken to a depth of 25 cm. Complete contents of each core were placed in separate plastic bags and gently sieved, in the laboratory, through 1 mm mesh. Sieve contents were held in bottles containing rose bengal in 10% buffered formalin until animal tissues were adequately stained and hardened. We later picked and identified to class (and to species in a subset of the samples) all animals in each sample.

In spring 1980, we also took 3 randomly located sediment cores (5 cm in diameter to a depth of 20 cm) from each matrix to characterize initial sediment conditions. Cores were transferred into individual plastic bags and frozen at −10°C until analysis of sediment size distribution by weight. We split each sample by coning and quartering (Ingram 1971) and then used standard Rotap dry sieving and pipetting procedures (Folk 1974) to estimate dry weights of sediments in each of several size classes. In addition, percent organic content was measured by weight loss on ignition at 550°C for 4 h (Gross 1981). Because our (customary) use of small-diameter cores to sample sediments failed to include large shell fragments and because such biogenic calcium carbonate appeared to be extremely common in 1 seagrass matrix, we designed a sampling procedure to estimate the relative degree of coarse shell. In October 1985, we used the suction dredge to excavate 3 haphazardly located 0.25 m^2 quadrats to a depth of 12 cm in each of the 6 matrices in each habitat. All shell fragments collected on a 3 mm

mesh were then cleaned with freshwater, dried at 60°C, and weighed to provide a quantitative indication of the relative degree of coarse shelliness in each matrix.

After our initial sampling in spring 1980, we applied harvest treatments on 2 occasions, 12-30 May 1980 and 19 December 1980-22 February 1981 with a single sampling of response variables in between (Table 1). We then sampled on 5 subsequent occasions to test for the existence and persistence of any treatment effects without applying any additional harvest treatments (Table 1). Of the 6 matrices in each habitat, 2 were left untouched as controls, 2 were given intense applications of "clam kicking", and the remaining 2 were subjected to lower but equal harvest intensities (judged by estimated percentage of spring 1980 *M. mercenaria* removed) of different types ("clam kicking" in one and hand raking in the other). Clam kicking is a mechanical form of clam harvest (described in detail in Guthrie and Lewis 1982) practiced in North Carolina which involves the modification of boat engines in such a way as to direct the propeller wash downwards instead of backwards. The propeller wash is sufficiently powerful in shallow water to suspend bottom sediments and clams into a plume in the water column, which allows *M. mercenaria* to be collected in a trawl net towed behind the boat (see Figure 2). To reproduce this process, we employed a commercial clam kicker and his boat. We measured in a crude way the relative intensity of the harvest treatment by counting all legally marketable (>2.54 cm in thickness in North Carolina) *M. mercenaria* removed and then estimating the percent removed of those available using the initial spring 1980 sampling (Table 2). We also recorded the number of

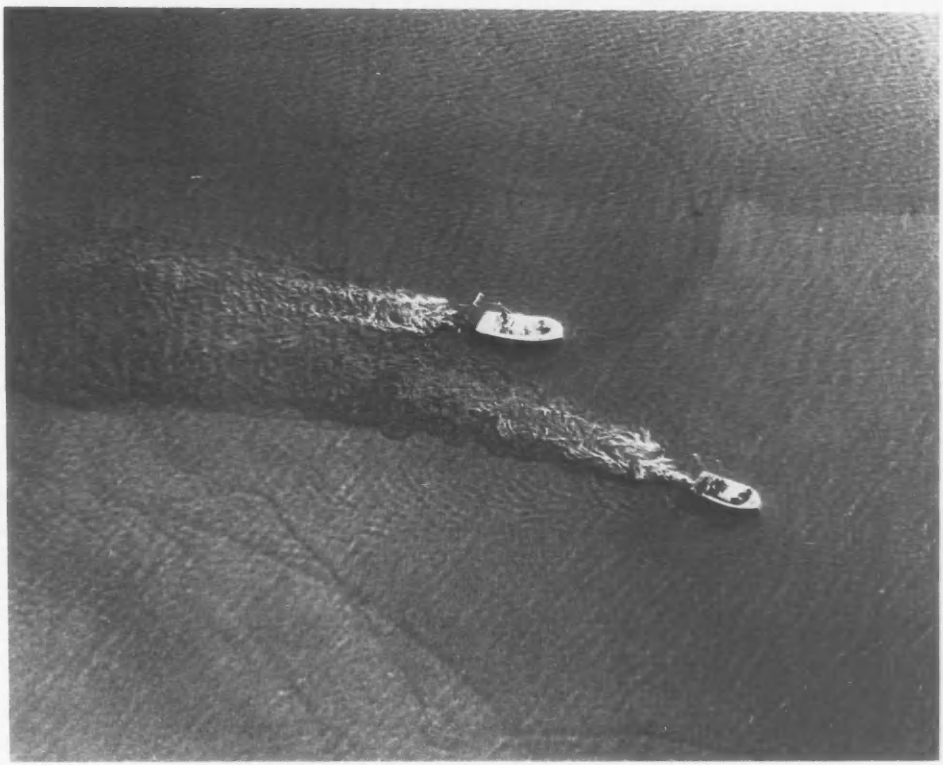

FIGURE 2.—Aerial photograph of a clam kicking boat in operation, showing the sediment plume in the wake and the tracks of previous kicking passes in the surrounding bottom.

TABLE 2.—The intensity of clam harvest treatments. All numbers and percents refer to legally harvested *Mercenaria mercenaria* >2.54 cm in thickness.

Habitat and harvest treatment	Treatment date and parameter estimated								
	May 1980			Winter 1980-81			Both applications pooled		
	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest
Sand flat									
Control I	0	0	0	0	0	0	0	0	0
Control II	0	0	0	0	0	0	0	0	0
Raking	191	16	170 min	140	11	210 min	331	27	380 min
Light-Kicking	140	17	2 passes 9 min	177	22	4 passes 30 min	317	39	6 passes 39 min
Intense-Kicking I	176	65	4 passes 20 min	165	61	3 passes 30 min	341	125	7 passes 50 min
Intense-Kicking II	384	47	8 passes 43 min	394	48	9 passes 87 min	778	95	17 passes 130 min
Seagrass bed									
Control I	0	0	0	0	0	0	0	0	0
Control II	0	0	0	0	0	0	0	0	0
Raking	134	1.9	275 min	925	13	2,125 min	1,059	15	2,400 min
Light-Kicking	91	1.4	2 passes 9 min	963	15	18 passes 121 min	1,054	16	20 passes 130 min
Intense-Kicking I	136	2.6	4 passes 22 min	2,608	49	32 passes 179 min	2,744	52	36 passes 201 min
Intense-Kicking II	1,033	12	12 passes 73 min	3,168	36	23 passes 156 min	4,201	48	35 passes 230 min

passes of the kicking boat and the minutes of clam kicking applied (Table 2). All *M. mercenaria* collected were returned to the laboratory for size-frequency estimates. The cumulative removals from the 2 clam harvesting applications produced relative treatment intensities acceptably close to our initial intentions (Table 2). For the hand raking treatment, we used short-handled rakes with 6-10 prongs of ≅14 cm in length separated by 3.5 cm gaps (see description and photograph of "pea digger" in Peterson et al. 1983a). We attempted to equalize the intensities of the raking and light-kicking treatments by removing equal percentages of the legally harvestable *M. mercenaria* from each of these two treatment matrices (Table 2). We also recorded the length of time actually spent raking as another indication of treatment intensity (Table 2).

RESULTS

Initial Sampling and Estimation of Shelliness

Within each habitat (sand flat and seagrass bed), one-way ANOVA was used on log $(x + 1)$-transformed data (which eliminated heteroscedacity in Cochran's tests) to assess whether any response variables differed significantly among the 6 matrices in spring 1980 prior to application of harvest treatments. There was no significant ($\alpha = 0.05$) initial variation among sand-flat matrices in any parameter: average total density of hard clams, average density of hard clam recruits (length <2.5 cm), average dry mass of seagrass, average density of all benthic macroinvertebrates, and sediment size (ϕ) (Table 3). Furthermore, the average percent organic content of sediments did not vary significantly among sand-flat matrices ($P > 0.05$ in ANOVA on angular-transformed proportions). Bay scallops were so rare in this initial sampling that we do not even record their densities in Table 3: bay scallops showed no significant difference among matrices in either habitat. The seagrass matrices exhibited significant initial variation in all parameters except average total density of hard clams and bay scallop density (Table 3). Variation in the other 4 parameters was not consistent across all seagrass matrices. A posteriori Duncan's tests, used to identify how specific seagrass matrices differed, show that the control II and raking matrices had significantly higher densities of hard clam recruits than all other seagrass matrices in spring 1980. Average seagrass biomass was significantly greater in intense-kicking I and significantly lower in control I than in all other seagrass matrices in the initial sampling. Control I also initially possessed a significantly higher average density of benthic macroinvertebrates, about 3 times the levels in the other seagrass matrices (Table 3). Duncan's test on mean ϕs revealed that in seagrass the raking and light-kicking matrices possessed

significantly higher initial ϕ values (finer sediments), although the differences among matrices were small. Percent organic content did not differ significantly ($P > 0.05$) among seagrass matrices in a one-way ANOVA on angular-transformed proportions.

The results of this initial sampling in spring 1980 prior to any application of clam harvest treatments imply that the sand-flat matrices were initially quite homogeneous. Consequently, any treatment effects can be expected to appear as significant differences that emerge among matrices in some or all samplings after application of the treatments. However, the initial differences among seagrass matrices imply that treatment effects may not be so readily identified. For those variables that exhibited initial differences among matrices, we performed two different tests of the effects of treatment. We performed simple ANOVA's to test for differences following treatment and we also, by subtraction of matrix means for spring 1980, adjusted the data from each matrix for initial differences and tested by ANOVA for significant changes in the differences among matrices. The first approach is appropriate if one believes that initial differences among matrices do not reflect intrinsic between-matrix differences that require adjustment, whereas the second approach assumes that initial differences among matrices would be expected to persist or recur in the absence of any treatment. An examination of how replicate matrices vary over time helps resolve which test procedure is more appropriate, but we performed both tests to provide a more robust set of conclusions.

Although all matrices in each habitat were chosen to be homogeneous in surface appearance, our October 1985 estimates of coarse shelliness of the surface (0-12 cm) sediments demonstrated that seagrass control I had almost 10 times the amount of coarse shell than any of the other seagrass matrices. The average (±SE) mass of shell fragments >3 mm in the top 12 cm of the 0.25 m^2 area in seagrass control I was 5,257 g (±701) compared with a range of 375 (±70) to 777 (±135) g across the other 5 seagrass matrices. This substantially larger amount of shell ($P < 0.001$ in a one-way ANOVA) seemed to be present during the entire experiment. Because surface shell fragments could greatly influence seagrass growth and especially *M. mercenaria* recruitment and survival (see Castagna and Kraeuter 1977), this physical anomaly of seagrass control I renders it a questionable control for the various treatment matrices. Similar data on surface shelliness taken from the sand matrices in October 1985 revealed no significant differences ($P > 0.05$) among matrices in a one-way ANOVA, with mean (±SE)

TABLE 3.—Contrasts among replicate matrices within each habitat before application of harvest treatments. Data are sample means (±SE) from spring 1980 (22 Feb.-6 May). Sample sizes appear in Table 1. Superscripts A and B indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly. Where ANOVA was non-significant, no means differ significantly.

	Habitat and sample average for each paramenter									
	Sand flat					Seagrass bed				
Future matrix designation	Total hard clam density per ¼ m^2	Density of hard clam recruits[1] per ¼ m^2	Seagrass dry mass (g per ¼ m^2)	Density of benthic inverte-brates per 0.008 m^2	Graphic mean sediment size (ϕ)	Total hard clam density per ¼ m^2	Density of hard clam recruits[1] per ¼ m^2	Seagrass dry mass (g per ¼ m^2)	Density of benthic inverte-brates per 0.008 m^2	Graphic mean sediment size (ϕ)
Control I	0.50 (0.14)	0.22 (0.10)	0.00	6.00 (1.34)	2.14 (0.00)	2.42 (0.44)	0.17^{B} (0.06)	10.36^{C} (2.38)	16.50^{A} (4.32)	2.75^{B} (0.21)
Control II	0.33 (0.10)	0.17 (0.07)	0.00	4.67 (0.76)	2.16 (0.03)	2.28 (1.72)	0.81^{A} (0.16)	14.37^{B} (2.23)	4.33^{B} (0.88)	2.94^{B} (0.12)
Raking	0.47 (0.13)	0.17 (0.06)	0.00	4.67 (0.84)	2.17 (0.04)	2.19 (0.38)	$0.53^{A,B}$ (0.14)	16.01^{B} (3.49)	4.83^{B} (1.11)	3.38^{A} (0.07)
Light-Kicking	0.25 (0.09)	0.06 (0.04)	0.00	6.00 (1.26)	2.16 (0.02)	2.28 (0.33)	0.39^{B} (0.11)	19.56^{B} (2.62)	5.67^{B} (2.08)	3.46^{A} (0.07)
Intense-Kicking I	0.36 (0.14)	0.17 (0.07)	0.00	3.17 (0.83)	2.10 (0.02)	1.83 (0.28)	0.39^{B} (0.10)	41.22^{A} (4.03)	6.50^{B} (1.52)	2.84^{B} (0.15)
Intense-Kicking II	0.47 (0.14)	0.17 (0.07)	0.00	5.67 (1.38)	2.18 (0.01)	2.56 (0.36)	0.27^{B} (0.09)	28.44^{B} (4.17)	5.67^{B} (2.33)	2.69^{B} (0.05)
Statistical significance[2]	NS	NS	NS	NS	NS	NS	***	***	*	**

[1]Recruits defined as <2.5 cm in length (see Peterson et al. 1983b for size data on 0 year class as support).
[2]* - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA comparing matrices before experimental initiation.

mass of shell fragments >3 mm ranging from 28 (±7) to 157 (±121) across the 6 sand-flat matrices.

Our field plots were closed to all commercial and recreational shellfishing during the 4 years of the experiment by proclamation of the North Carolina Division of Marine Fisheries to avoid disruption of the experiments. However, on 7 occasions out of 50 days of observation, we observed clammers within the boundaries of our plots: 5 times in seagrass control matrix I and once in both the seagrass raking matrix and the intense-kicking II matrix. This represents significantly more illegal clamming in control I than would be expected by chance alone ($P < 0.01$ in a binomial test). Thus, the seagrass control I matrix may not represent a true control for our experiment.

Posttreatment Sampling

Mercenaria mercenaria Recruitment

In the sand-flat habitat there were only two Octobers during which *M. mercenaria* recruits were sampled: October 1980 after the initial application of the clam harvest treatments and October 1981 after both treatment applications. In neither sampling did a one-way ANOVA on log (x + 1)-transformed counts (which removed heteroscedacity in Cochran's tests) reveal significant ($\alpha = 0.05$) variation in average density of recruits among sand-flat matrices (Table 4). Furthermore, a two-way ANOVA on log (x + 1)-transformed counts from both time periods, done to increase the power of the test of matrix differences, also failed to reveal any significant variation in average recruitment among sand-flat matrices. Despite the failure to demonstrate statistical significance in *M. mercenaria* recruitment among sand-flat matrices, the average density of recruits in the control matrices during these two Octobers was more than double (on untransformed scale) the average density in the 2 high-intensity clam kicking matrices (Fig. 3). Some of this difference may have been present even before treatments were applied (Fig. 3), but it is also possible that the high local variability in recruitment lowers the power of this test of harvest treatment to a degree that even a twofold difference is undetectable.

During 4 Octobers, *M. mercenaria* recruitment was estimated in the seagrass habitat (Table 4). One of these, October 1980, fell after the first harvest treatment (which Table 2 shows to have been very light in the seagrass plots) but before the second, more intense treatment. The other 3 samplings came in successive years, increasingly far from the actual time of application of the harvest treatments. Because of the preexisting significant differences

TABLE 4.—The impact of clam harvesting on recruitment of *Mercenaria mercenaria*. Entries are mean numbers (±SE) of recruits per ¼ m^2. Recruits are defined as all individuals <2.5 cm in length in October of each year. For 1980 and 1981, n = 36 samples from each treatment matrix in each habitat, whereas for 1982 and 1983, n = 9 for seagrass and 0 for sand flat.

	Habitat and date							
	Sand flat			Seagrass bed				
Treatment matrix	1980	1981	Unweighted average	1980	1981	1982	1983	Unweighted average
Control I	0.33 (0.11)	0.17 (0.06)	0.25	0.94 (0.21)	0.61^{A} (0.13)	$0.67^{A,B}$ (0.24)	0.67 (0.24)	0.72
Control II	0.36 (0.11)	0.06 (0.04)	0.21	0.72 (0.15)	0.28^{B} (0.09)	$1.33^{A,B}$ (0.47)	1.56 (0.77)	0.97
Raking	0.44 (0.13)	0.14 (0.08)	0.29	0.81 (0.14)	0.22^{B} (0.07)	$0.78^{A,B}$ (0.32)	1.67 (0.55)	0.87
Light-Kicking	0.19 (0.08)	0.08 (0.05)	0.14	0.61 (0.13)	0.11^{B} (0.05)	2.11^{A} (0.68)	0.33 (0.17)	0.79
Intense-Kicking I	0.11 (0.05)	0.03 (0.03)	0.07	0.42 (0.11)	$0.39^{A,B}$ (0.10)	0.22^{B} (0.15)	0.67 (0.17)	0.43
Intense-Kicking II	0.22 (0.07)	0.08 (0.05)	0.15	0.56 (0.14)	$0.33^{A,B}$ (0.10)	0.56^{B} (0.24)	0.33 (0.24)	0.45
Statistical significance[1]	NS	NS	NS	NS	**	*	NS	*

[1] * - $P < 0.05$, ** - $P < 0.01$ in one-way ANOVA's on each date and two-way ANOVA's over all dates, reported in the unweighted average column. These analyses were performed on log-transformed data, which eliminated or reduced heteroscedacity in Cochran's tests. Superscripts A and B indicate significant differences in Duncan's test at $\alpha = 0.05$. No Duncan's test results are given for the unweighted averages in the seagrass bed because the two-way ANOVA exhibited highly significant ($P < 0.001$) interaction between date and treatment.

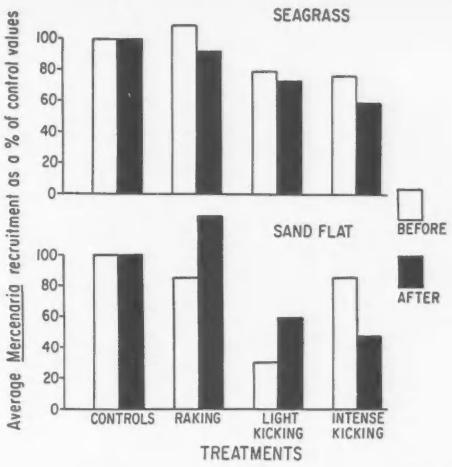

FIGURE 3.—Average density of *Mercenaria* recruits (<2.5 cm in length) before harvest treatments in spring 1980 and after in October 1980 and 1981 (averaged together). ANOVA's showed no significant effect in the sand flat but several significant changes after treatment in the seagrass bed (see Table 4). Seagrass matrices are grouped together for illustration of effects on the basis of results of Duncan's tests performed on 1980 and 1981 data adjusted for spring 1980 differences in recruit densities. Consequently, these groupings separate those seagrass matrices that changed in recruitment pattern after treatment.

among seagrass matrices in *M. mercenaria* recruitment, we analyzed the posttreatment data by both simple ANOVA to test for differences in each postharvest sampling and by ANOVA on adjusted data to test for significant changes away from the initial differences. The results of these two different sorts of analysis were inconsistent. ANOVA's on simple recruit densities [log $(x + 1)$-transformed, which homogenized variances in Cochran's tests] demonstrated significant differences among matrices in October 1981 and 1982, but not in 1980 or 1983. Duncan's tests on the 1981 and 1982 results showed few significant differences and no consistent difference in these 2 years (Table 4). The unweighted means suggest that *M. mercenaria* recruitment may have been less in the 2 intensely kicked matrices, but the two-way ANOVA had a significant date by treatment interaction preventing application of Duncan's test.

Despite an indication of lower *M. mercenaria* recruitment in the 2 intensely kicked matrices (Table 4), ANOVA's performed on recruit data adjusted for initial differences among matrices to test whether those differences changed after treatment revealed a different pattern. Only the 1980 and 1981 results were significant (both at $P < 0.001$). The patterns of change in recruitment among matrices were the same in Duncan's tests on both 1980 and 1981 data (Fig. 3). The shelly control I exhibited over 4 times as much recruitment in October 1980 and 1981 as in spring 1980, while control II exhibited about a 40% decrease after harvest (Fig. 3). Raking and light-kicking matrices behaved similarly, showing about the same value after harvest as before. The 2 intense-kicking matrices showed about a 30% increase in *M. mercenaria* recruitment after harvest (Fig. 3). Thus, the ANOVA's on adjusted data produce results dependent upon whether control I is discarded or averaged together with control II.

This demonstrates that conclusions about how clam harvest affects *M. mercenaria* recruitment are not robust to the decision of how to treat the shelly control or to the relaxation of the assumption that matrices are expected to repeat any initial differences in recruitment in the absence of treatment as an intrinsic characteristic. The choice of analysis might be made by examining whether matrices that are treated identically show similar or dissimilar patterns of recruitment in different years. A comparison of all posttreatment recruit data in the 2 intensely kicked matrices (Table 4) reveals that they never differed from one another significantly, although the mean difference and even ranking between them varied. The 2 control matrices diverged radically from one another (Table 4), but unpredictable illegal clamming in matrix I may be at least partly responsible. Because of the ambiguities in these data, it is impossible to draw any firm conclusion on how treatments affected *M. mercenaria* recruitment in the seagrass.

Seagrass Biomass

Because of substantial and significant differences among seagrass matrices in seagrass biomass in spring 1980 before application of any treatment, we analyzed the posttreatment data by both simple ANOVA to identify significant differences among matrices after treatment and also by ANOVA on adjusted observations to test for significant change in the initial pattern of biomass differences among matrices. The results of these 2 types of analysis are qualitatively identical, so we present only the results on adjusted data. We prefer this analysis because the *Zostera marina* and *Halodule wrightii* in North Carolina are perenials that do not readily and quickly spread into new areas (Thayer et al. 1985), so that initial patterns of difference in seagrass biomass

might be expected to persist in the absence of treatment effects. All ANOVA's were performed on untransformed data (seagrass biomass or differences in seagrass biomass) because Cochran's test for heteroscedacity was nonsignificant on 2 of the 6 data sets and log and square root transformations failed to reduce the significance level ($P < 0.05$ on 2 and $P < 0.01$ on the other 2).

There was a clear and large effect of intense kicking. The ANOVA's on adjusted data were highly significant for every posttreatment sampling date, indicating that the initial differences among seagrass matrices in average seagrass biomass shifted significantly after application of harvest treatment and never returned to initial levels even by fall 1984. The 2 intense-kicking treatments had consistently low seagrass even after the first light treatment but especially after both treatment applications. Light kicking and raking never differed significantly from one another in seagrass biomass. The shelly control I matrix diverged from the other control (II) in having low values in all posttreatment samplings, often grouping with the 2 intense-kicking matrices in the Duncan's test (Table 5).

Average biomass of seagrass in each treatment matrix is compared in Figure 4 to the changes that would be predicted from the average biomass in the 2 untreated control matrices. This approach smoothes out the seasonality and other temporal variability by normalizing all the treatment means to the control values. It assumes that the differences among matrices observed in spring 1980 in average biomass would be expected to persist indefinitely and then calculates what percent of the expected seagrass biomass each treatment matrix actually exhibited on each sampling date. This assumption is clearly violated by the divergent behavior of the 2 control matrices, but it provides a conservative estimate of the effects of harvest because the average of the 2 controls includes control matrix I, which exhibited low seagrass biomass, perhaps because of enhanced illegal clamming. Clam harvest treatments immediately reduced seagrass biomass below the expected amounts, with greater effects of the second, more intense (see Table 2), harvest treatments. The 2 intense clam-kicking treatments exhibited a decline of about 65% in expected biomass from spring 1980 until spring 1981, while biomass declined by about 25% below expected in the raking and light-kicking matrices. Seagrass biomass recovered to equal and even exceed expected values by the very next sampling period in fall 1981 in the raking and light-kicking matrices, and remained high for the next 3 years. However, recovery in seagrass biomass in the 2 intense-kicking matrices did not begin to occur until sometime in fall 1982-fall 1983 (Fig. 4) and was not yet complete by fall 1984. In fall 1984, almost 4 years after the second harvest treatment, average biomass of seagrass in the 2 intense-kicking plots was only 65% of the expected levels. These estimates are conservative if the shelly control (I) matrix is actually a poor control for this experiment because we used the mean of both controls as an expected value for Figure 4. Scheffé a priori contrasts of matrix means (in Table 5) show that, despite the divergence of the 2 controls, the mean seagrass biomass was significantly ($P > 0.05$) less in the 2 intense-kicking matrices than expected from the 2 controls in all sampling periods after application of both harvest treatments. This test provides the statistical justification for our presentation of differences in Figure 4.

TABLE 5.—The impact of clam harvesting on the average seagrass dry mass (± SE) per ¼ m^2 within the seagrass habitat. Data presented for each date and matrix are the mean (± SE) dry mass of seagrass per sample minus the mean dry mass in spring 1980 for that particular matrix (from Table 3). Sample sizes appear in Table 1. Clam harvesting treatments occurred between spring 1980 and fall 1980 and again between fall 1980 and spring 1981. Superscripts A-D indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

Treatment matrices	Fall 1980	Spring 1981	Fall 1981	Fall 1982	Fall 1983	Fall 1984
Control I	2.2(2.9)^{C,D}	19.5(11.2)^{A}	7.4(3.3)^{B}	11.9(6.1)^{A}	1.2(4.4)^{B}	8.0(7.2)^{B}
Control II	19.7(2.7)^{A}	25.8(4.0)^{A}	20.0(2.0)^{A}	22.8(5.2)^{A}	40.1(5.9)^{A}	40.8(3.8)^{A}
Raking	7.7(1.8)^{B,C}	10.5(3.2)^{A}	15.2(2.0)^{A,B}	13.6(5.1)^{A}	38.2(7.0)^{A}	41.1(5.4)^{A}
Light-Kicking	13.8(2.9)^{A,B}	14.4(6.0)^{A}	15.3(3.0)^{A,B}	13.6(3.5)^{A}	31.9(4.7)^{A}	35.7(5.1)^{A}
Intense-Kicking I	−1.5(2.7)^{D}	−21.2(6.9)^{B}	−18.8(4.3)^{C}	−29.0(6.1)^{C}	−18.8(6.0)^{C}	5.6(9.1)^{B}
Intense-Kicking II	7.1(3.7)^{B,C}	−9.1(5.4)^{B}	−12.2(3.1)^{C}	−11.3(7.2)^{B}	9.2(10.8)^{B}	1.5(4.4)^{B}
Statistical significance[1]	***	***	***	***	***	***

[1] *** - $P < 0.001$ in one-way ANOVA's on untransformed dry masses, comparing the matrix means on each separate date. ANOVA's were performed on the differences from spring 1980 matrix means because of pre-existing significant differences among matrices in spring 1980 before application of harvest treatments.

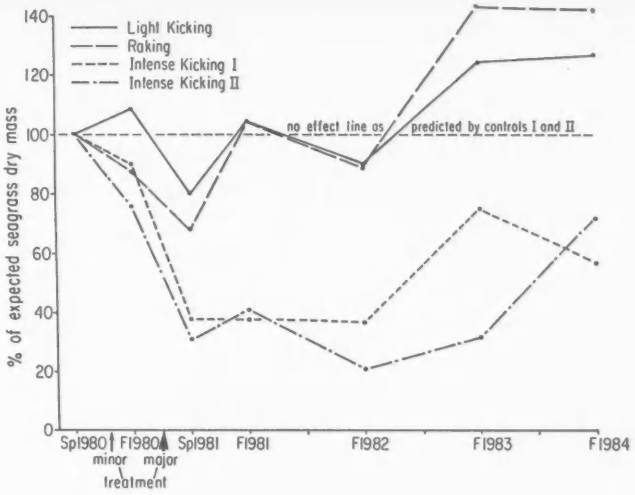

FIGURE 4.—Percent difference between observed average biomass of seagrass in each treatment matrix and expected biomass based on the assumption that initial differences between the two control matrices and each treatment matrix would be expected to remain constant across time. The expected biomass is then plotted as 100% (the no effect line). Times of the two clam harvest treatments are indicated with arrows on the x-axis.

Benthic Macroinvertebrates

In the sand-flat habitat, the average density of benthic macroinvertebrates never varied significantly among matrices (Table 6) in any of the 3 posttreatment sampling dates [one-way ANOVA's were run on log $(x + 1)$-transformed counts, using a separate analysis for each date]. The sums over all 3 posttreatment dates of the average macroinvertebrate densities per core are nearly identical for each sand-flat matrix and a two-way ANOVA on log $(x + 1)$-transformed densities from all 3 time periods revealed no significant difference among matrices.

In the seagrass habitat, analogous one-way ANOVA's done separately for each date, demonstrated that the average density of benthic macroinvertebrates did not differ significantly among seagrass matrices in fall 1980 or spring 1981 (Table 6). A significant difference among matrices did appear in fall 1981, and in a two-way ANOVA on all 3 posttreatment dates together. Despite the statistical significance of 2 of 4 ANOVA's, actual differences in mean densities among seagrass matrices were proportionately small. Furthermore, Duncan's tests revealed a pattern of differences among matrices (Table 6) that was identical to the initial pattern of significant differences in the spring 1980 sampling before treatment (see Table 3).

Although the sums of the sample means from each of the 3 posttreatment sampling dates (Table 6) imply that benthic macroinvertebrate densities in the seagrass habitat were about double those in the sand flat, this pattern was not consistent across seasons. Nested ANOVA's, done on log $(x + 1)$-transformed counts and performed separately for each sampling date, showed that there was no significant difference between habitats during either spring sampling period (spring 1980 or 1981), whereas average densities of benthic macroinvertebrates were significantly greater ($P < 0.001$ in fall 1980 and $P < 0.005$ in fall 1981) in the seagrass habitat in both of the Octobers.

Although the clam harvesting treatments did not affect total density of benthic macroinvertebrates in either habitat, species composition might still have been altered. We identified all individuals in 16 cores in each habitat from the spring 1980 pretreatment sampling (4 cores randomly chosen from each control matrix and from each intense-kicking matrix) and in 16 cores in each habitat from the spring 1981 posttreatment sampling (drawn equally from each of the same matrices). This comparison holds season constant and permits us to test for any gross shifts

TABLE 6.—The impact of clam harvesting on average density (± SE) of benthic macroinvertebrates per 0.008 m^2. n = 6 samples for each treatment matrix at each sampling date. Samples were taken to 25 cm and passed through 1 mm mesh. Superscripts A-C indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

	Habitat and date							
	Sand flat				Seagrass bed			
Treatment matrix	Fall 1980	Spring 1981	Fall 1981	Sum	Fall 1980	Spring 1981	Fall 1981	Sum
Control I	8.0 (2.7)	5.7 (1.2)	8.0 (1.4)	21.7	34.3 (7.8)	9.3 (1.8)	16.2^{A} (2.9)	59.8^{A}
Control II	11.7 (1.5)	7.7 (1.4)	4.2 (0.8)	23.6	19.0 (2.0)	10.5 (1.6)	$11.0^{A,B}$ (1.6)	40.5^{B}
Raking	6.5 (0.5)	8.2 (1.0)	4.8 (0.8)	19.5	39.8 (5.1)	6.8 (1.1)	$12.0^{A,B}$ (2.4)	58.6^{B}
Light-Kicking	12.3 (2.6)	11.5 (3.0)	4.5 (0.9)	28.3	29.5 (8.6)	5.8 (1.3)	$7.8^{B,C}$ (1.3)	44.1^{B}
Intense-Kicking I	7.8 (0.7)	8.7 (1.7)	6.3 (1.4)	22.8	23.5 (4.8)	8.7 (2.9)	6.5^{C} (1.2)	38.7^{B}
Intense-Kicking II	9.7 (2.2)	6.0 (1.3)	5.0 (0.8)	20.7	34.5 (10.7)	6.3 (1.1)	6.0^{C} (0.9)	46.8^{B}
Statistical significance[1]	NS	NS	NS	NS	NS	NS	**	***

[1] ** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA's (for each separate date) and two-way ANOVA's (for sums) on average macroinvertebrate counts per core (transformed by log (x + 1)).

in species composition as a function of the intense-kicking treatment. Table 7 presents the results of these species identifications and shows that no major shift in species composition of the most abundant species occurred in either the sand-flat or seagrass habitat following the application of the intense-kicking treatment. Polychaetes dominated the fauna of both habitats and the same species of polychaetes tended to be represented at similar densities both before and after intense clam kicking.

Bay Scallop Densities

Bay scallops were never encountered in sampling the sand-flat matrices, so we have no test of whether clam harvest treatment affects bay scallops in areas lacking seagrass. One-way ANOVA's on log (x + 1)-transformed counts (which removed heteroscedacity in Cochran's tests) demonstrated significant (α = 0.05) differences among seagrass matrices in average bay scallop density on only 2 sampling dates, fall 1980 and fall 1983 (Table 8). Duncan's test on the fall 1980 data showed that bay scallop density in control I was significantly ($P < 0.05$) lower than in every other matrix except intense-kicking II, and that there were no other significant differences between pairs of matrices. Because the fall 1980 sampling occurred before the major application of clam harvest treatments (see Table 2), this sampling period may be considered a pretreatment sampling. Extremely low seagrass biomass in control I in fall 1980 (Table 5) may explain the significantly lower bay scallop densities in that matrix on that date.

The fall 1983 sampling occurred after a period of more successful bay scallop recruitment than occurred before any other sampling date (Table 8) and, thus, provided more "substrate" on which effects of clam harvest treatments may have operated. Duncan's test on mean bay scallop densities for fall 1983 demonstrated that the matrices split into two separate groups: a low-density group, made up of control I and the 2 intense-kicking matrices, and a high-density group, comprised of control II, the raking, and light-kicking matrices (Table 8). Within each group, no matrices differed significantly (α = 0.05) from any other, but all differences between groups were statistically significant. Because fall 1983 bay scallop densities were so much greater than at any other sampling date, the sums over all five sampling periods also exhibited significant differences among matrices in an analogous two-way ANOVA, and Duncan's tests separated the matrices into groupings virtually identical to those detected for the fall 1983 data set alone (Table 8).

A contrast of the bay scallop results of fall 1980 and fall 1983 demonstrates that after application of the second intense-kicking treatment in the seagrass habitat in winter of 1980-81, bay scallop densities declined to join the already low value of control I,

which together formed a group of low-density bay scallop matrices. About 84% of the variance in bay scallop densities in fall 1983 is explained by seagrass biomass in a simple linear regression. Figure 5 presents the relationship between average seagrass biomass and bay scallop densities on a 1,225 m^2 scale, which suggests that the 2 intense-kicking matrices contained even fewer bay scallops than predicted from their reduced seagrass biomass. This is similarly illustrated from calculations of the mean numbers of bay scallops per 100 g of seagrass in each matrix in fall 1983: control I (5.7), control II (5.1), raking (4.7), light kicking (4.3), intense-kicking I (2.0), and intense-kicking II (2.3).

TABLE 7.—For each habitat, total numbers of individuals found in four randomly chosen cores from each of the two controls and the two intense-kicking matrices on two dates, one before and one after clam-harvest treatment. All species with total counts greater than two are listed separately.

Species	Spring 1980 Before treatment		Spring 1981 After treatment	
	Controls	Intense-kicking	Controls	Intense-kicking
Sand-flat habitat				
Aricidia fragilis	7	1	6	5
Notomastus hemipodus	3	4	5	5
Platynereis dumerilii	1	0	5	7
Axiothella sp.	3	2	1	7
Drilonereis magna	5	5	0	1
Spiochaetopterus oculata	0	2	3	3
Arabella iricolor	3	1	1	2
Glycera sp.	5	1	0	0
Others[1]	5	2	2	1
Seagrass habitat				
Axiothella sp.	23	8	7	4
Platynereis dumerilii	12	8	14	1
Notomastus hemipodus	20	7	4	0
Tharynx marioni	3	4	3	2
Nereis falsa	0	1	5	5
Glycera sp.	3	4	2	1
Melinna maculata	1	0	6	3
Onuphis jenneri	0	1	3	3
Lumbrinereis sp.	0	0	4	3
Spiochaetopterus oculata	1	0	4	0
Spionidae	4	0	0	1
Sthenelais limicola	0	1	1	1
Arabella iricolor	0	2	1	0
Poecilochaetus sp.	3	0	0	0
Onuphidae	0	0	3	0
Others[1]	1	2	1	1

[1]These include molluscs, an amphipod, and additional polychaetes.

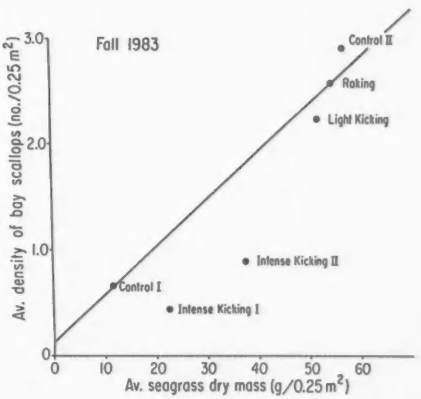

FIGURE 5.—Relationship between the average density of bay scallops, *Argopecten irradians*, and the average biomass of seagrass in fall 1983 samplings of each control and treatment matrix of the clam harvest experiment in the seagrass matrix. Clam harvest treatments had been applied in spring 1980 and again in winter 1980-81.

TABLE 8.—The effect of clam harvesting in the seagrass habitat on average bay scallop, *Argopecten irradians*, density per ¼ m^2 (±SE). Sample sizes per treatment matrix were 36 in fall 1980 and fall 1981 and 9 in spring 1981, fall 1982, and fall 1983. No data are presented for the sand flat because of the rarity of bay scallops in that habitat. Superscripts A-C indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

Treatment matrix	Sampling date					
	Fall 1980	Spring 1981	Fall 1981	Fall 1982	Fall 1983	Sum
Control I	0.11(±0.05)^{B}	0.44(±0.24)	0.05(±0.04)	0.11(±0.16)	0.66(±0.33)^{B}	1.37^{C}
Control II	0.63(±0.11)^{A}	1.00(±0.37)	0.14(±0.07)	0.22(±0.15)	2.89(±0.51)^{A}	4.88^{A}
Raking	0.53(±0.14)^{A}	0.78(±0.28)	0.16(±0.06)	0.44(±0.24)	2.56(±0.67)^{A}	4.47^{A}
Light-Kicking	0.75(±0.18)^{A}	0.33(±0.33)	0.14(±0.07)	0.89(±0.42)	2.22(±0.46)^{A}	4.33^{A}
Intense-Kicking I	0.50(±0.12)^{A}	0.22(±0.15)	0.03(±0.03)	0.00(±0.00)	0.44(±0.29)^{B}	1.19^{B,C}
Intense-Kicking II	0.39(±0.11)^{A,B}	0.56(±0.18)	0.14(±0.07)	0.55(±0.24)	0.88(±0.35)^{B}	2.52^{B}
Statistical significance[1]	**	NS	NS	NS	***	***

[1]** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA on log $(x + 1)$-transformed sample counts, comparing matrix means on each date and in a two-way ANOVA over all dates (in the sums column).

DISCUSSION

The one-way ANOVA's which we performed to test the significance of differences in parameter means among matrices at any given sampling date can demonstrate heterogeneity among matrices. If there is no significant heterogeneity, we probably can conclude safely that there was no effect of treatment on that parameter at that sampling date, assuming that equivalent levels of the parameter prevailed before application of the treatment (which was not always true). If, on the other hand, the one-way ANOVA demonstrates significant differences among matrices, this result does not necessarily imply that the treatment was the cause. Replication in these ANOVA's is generated from subsamples within each individual matrix. These subsamples taken from within a given matrix are not independent because of their spatial proximity. Consequently, matrices can diverge in various ways from one another over the course of an experiment, caused by extraneous events that act on the scale of the plot (matrix) to destroy independence among subsamples. This experimental design would be termed pseudoreplication (Hurlbert 1984), and permits a test of whether plots differ significantly and does not allow an unambiguous assignment of observed differences to the treatment applied (but see Stewart-Oaten et al. 1986). For that reason, we replicated both our control matrices and our intense-kicking matrices in each habitat. These permit us to use a priori contrasts, with replication of 2 separate, independent plots, to test unambiguously whether the most important treatment (intense clam kicking) was responsible for observed changes. Appreciation of the differences between these two sorts of analyses is necessary to interpret properly the results of this study.

Although we designate our heavier clam-kicking treatment "intense", it probably falls well short of the effort that commercial clammers would apply to a productive seagrass bottom; we took only an estimated 50% of the clams legally available for harvest (Table 2). Consequently, the intensity of harvest that we applied in the seagrass is not unreasonably high. In the sand-flat system, we took approximately 100% of the estimated numbers of legally available clams in our intense treatments. Although higher than the percent taken in the seagrass, this probably better approximates the fishing intensity that is applied to productive unvegetated areas by commercial clammers. Efficiency of returns remained high even in the high-intensity kicking matrices, as compared with hand raking. In the sand flat, light kicking produced an average of 8.1 clams per minute and intense kicking 6.2 clams per minute, compared with a return of only 0.9 clams per minute from hand raking (Table 2). In the seagrass bed, light kicking yielded an average of 8.1 clams per minute and intense kicking 16.1 clams per minute, in contrast to a return of only 0.4 clams per minute from hand raking (Table 2). Thus, efficiency of harvest, defined as clams caught per unit of time, was clearly greater by over an order of magnitude with the mechanical technique than with the traditional hand method. The improved efficiency during clam kicking in the seagrass as harvest intensity increased from taking about 15% to about 50% of available clams is probably caused by the gradual removal of seagrasses which, when present, reduce the efficiency of clamming.

To test whether hard clam harvest affects its own recruitment in the area of harvest, we counted new recruits (<2.5 cm in length, Peterson et al. 1983b). Recruitment, when estimated in this fashion, confounds both larval (and postlarval) settlement with subsequent early mortality from time of settlement until October. Consequently, we do not directly test the hypothesis that natural densities of adult hard clams inhibit larval settlement in their vicinity. Furthermore, our clam harvest treatment not only removes many larger hard clams, but it also disturbs the bottom sediments. Consequently, there are several plausible mechanisms by which our clam harvest treatments may affect October recruitment of hard clams: 1) reduction of adult hard clam density may affect hard clam settlement (positively, if negative adult-larval interactions predominate, as suggested by most past studies: Woodin 1976; Williams 1981; Peterson 1982b) or survivorship from settlement until October (no a priori prediction from the literature on what direction this effect may take), or 2) disturbance of the bottom may alter hard clam settlement (positively, if hard clam larvae select disturbed sediments, which seems unlikely, or negatively if hard clam larvae avoid disturbed sediments) or early survivorship (negatively, if the clam harvest buries small clams too deeply to reemerge or if disturbance has removed protective seagrass or shell materials and thereby made juvenile hard clams more vulnerable to predators (Peterson 1982a; Summerson and Peterson 1984)).

Our data on hard clam recruitment are sufficiently ambiguous to preclude any definitive answers to the question of how clam harvest affects subsequent recruitment. In the sand flat, there was no significant effect of harvest treatment, but the 2 intensely kicked matrices yielded only 50% of the recruits

produced by the 2 controls (Fig. 3). In the seagrass, *M. mercenaria* recruitment may also have been reduced by harvest treatments (Table 4), but the conclusion depends upon the assumption that the shelly control I was an adequate control for recruitment data. Given the enhanced survivorship of *M. mercenaria* recruits in shell (Castagna and Kraeuter 1977) and the significant illegal clamming in seagrass control I, this assumption is questionable.

It is possible that removal of adult hard clams enhances larval settlement over a larger spatial scale than the 1,225 m^2 experimental plots because depletion of larvae by feeding from the water column should extend over a larger spatial scale (Peterson 1982b). Although it is possible that our sampling was on too fine a scale to detect such an effect, our sampling occurred on a far larger spatial scale by 3 orders of magnitude than any previous experimental test of adult-larval interactions and, thus, should have provided for greater opportunity to detect any positive effect of adult hard clam removal. The failure to demonstrate a response in the sand flat may be a different consequence of scale. Newly recruited hard clams may settle more heavily where adult densities have been reduced but the effect may be diffused away by the physical dispersal of new recruits by tidal currents and waves. As a consequence of such multiple interpretations, we can best conclude that on the scale of our experiments no dramatic increase in hard clam recruitment occurs with intense mechanical harvest of adult hard clams in seagrass and harvest may even reduce recruitment in both unvegetated and vegetated areas.

The effect of various clam harvest treatments in the seagrass bed on seagrass biomass (Fig. 4) is the most obvious result of this study. Clam harvest of all types had an immediate impact in reducing the seagrass biomass. Reduction of seagrass increased with harvest intensity, as was demonstrated both by the enhanced effect of the second treatment application, which was much more intense than the first, and also by the larger effects of intense kicking as compared with the other treatments (Fig. 4). Although the seagrass biomass in the raking and light-kicking matrices recovered to levels predicted from the controls within a year's time, the seagrass biomass in the intense-kicking matrices did not even begin to recover for 2 years and had not fully returned to predicted, control levels after 4 years. These results imply that if sufficient seagrass is destroyed, recovery is slow. Because our intense-kicking treatment removed only an estimated 50% of available hard clams and because the efficiency of hard clam capture per unit time of harvest was greater in the intense treatment than in the light treatment in the seagrass habitat, we suspect that commercial clam kickers would apply even more harvest intensity than we did in the this intense-kicking treatment. Consequently, the effects of commercial clam kicking in seagrass beds are probably underestimated by our data (Fig. 4). Furthermore, by using both control matrices (including the shelly one) in estimating the effects of harvest on seagrass biomass, we intentionally provide an additional conservative bias. Clam kicking at a low level (≅15% of available hard clams harvested) does not appear to be any more destructive of seagrass than hand raking that same number of clams, but the lack of replication of these two types of treatment matrices renders this a tentative conclusion.

The extremely slow recovery of seagrass in the intensely kicked seagrass matrices raises the possibility that seagrass beds and unvegetated sand flats may exist as alternative stable states (Sutherland 1974; Connell and Sousa 1983; Peterson 1984) on many of the same shallow bottoms of sounds and coastal lagoons. That is, a given shallow bottom may exist as either a seagrass bed or an unvegetated sand flat, but whichever state it occupies it is likely to retain for a relatively long period of time. Transformation from one state to another may require some input of external energy. Because great changes in current regime and surface sediment character are associated with the presence and growth of seagrasses (Ginsburg and Lowenstam 1958; Orth 1977; Fonseca et al. 1983; Peterson et al. 1984; Eckman in press), it is reasonable to hypothesize that destruction of seagrass may result in sufficiently higher energy at that site that natural reestablishment could be difficult. Certainly, the slow return of seagrass following intense clam kicking in our experiments implies that seagrass recovery even in previously vegetated areas is tenuous. If seagrass beds and unvegetated bottoms do tend to represent alternative stable states for large areas of the estuarine and sound bottom, then denuding of vegetation would have long-lasting effects, even beyond what we have demonstrated. Furthermore, transplantation of relatively dense seagrass may be necessary to produce rapid reversion back into a vegetated system (for reviews of disturbance, recovery, and transplantation of seagrasses see Zieman 1982; Thayer et al. 1985). Because of the important roles that seagrasses play in promoting estuarine productivity and coastal fisheries (Thayer et al. 1975), intense clam kicking in vegetated areas could have long-lasting and

serious impacts on many commercially important fisheries. Our own data imply a potentially negative impact on hard clam recruitment (Table 4) and a clear reduction in bay scallop abundance (Table 8) in part because of reduction in seagrass biomass.

Clam harvesting had no detectable effect on the abundance of small benthic invertebrates. The density data did not even suggest an effect (Table 6) and the composition of the most abundant species did not change, even with intense clam kicking (Table 7). This lack of response is probably a consequence of the dominance of small polychaetes in these invertebrate data. Small polychaetes make up most of the total infaunal density and all of the most abundant species. Small polychaetes tend to exhibit rapid turnover, quick colonization and short life spans, relative to molluscs, echinoderms, and many other invertebrates; consequently, they may be expected to recover more rapidly after disturbance. The large seasonal variability in total macroinvertebrate density at our seagrass sites is a reflection of the short-term response times of this fauna, which is known to exhibit large seasonal fluctuations in density in North Carolina (Commito 1974).

Like several previous studies of the densities of benthic infauna (Kikuchi 1966; Warme 1971; Orth 1977; Reise 1977, 1978; Stoner 1980; Summerson and Peterson 1984), our data demonstrate higher densities inside the seagrass bed than on unvegetated bottoms in October. However, the difference in infaunal density between habitats appears to vary seasonally, as shown previously (Reise 1978; Stoner 1980). In spring, the two habitats had approximately equal densities of infauna. Because estuarine densities of epibenthic predators, both fishes (Adams 1976; Orth and Heck 1980) and crustaceans (Heck and Orth 1980), also vary seasonally such that our fall samplings occur after months of high density and our spring samplings after a low-density season for epibenthic consumers, these new observations provide further support for the hypothesis (see review of concepts in Kikuchi 1980; experimental evidence in Reise 1977; Orth 1977; Summerson and Peterson 1984) that seagrass provides a natural refuge from predation for infaunal invertebrates.

Intense clam kicking caused a substantial decline in the average density of bay scallops in the seagrass habitat (Table 8). Most of the variation among matrices in the total densities of bay scallops and in the fall 1983 densities, when numbers were high, could be readily explained by the variation among matrices in average seagrass biomass. Bay scallops recruit to seagrass blades where they remain attached by byssal threads for the first few months of life. In addition, adult bay scallops, which are mobile, tend to be found in seagrass beds, as our failure to encounter them in the sand-flat samples illustrates. Their feeding may be more efficient in the slower currents of the seagrass environment (Kirby-Smith 1972). Consequently, it is not surprising that reductions in bay scallop density accompanied the declines in average seagrass biomass in our experiments. However, the apparent effect (Fig. 5) of intense clam kicking that persists even after the seagrass biomass effect is removed was a surprise. Because the application of clam kicking is necessarily patchy (it forms a trail behind the path of the boat) and, thus, produces an increase in the patchiness of the vegetation (see standard errors in Table 5), we suspect that this residual effect of intense clam kicking is a reflection of that enhanced seagrass patchiness. We hypothesize that the average biomass of seagrass present in our plots is more attractive (in a broad sense) to bay scallops when it is more uniformly distributed over a given area than when it is clumped into more discrete patches at least on the 0.25 m^2 scale of our samples.

The implications of this study for the management of the hard clam fishery depend upon the specific values attributed to various factors. Our data show clearly the enhanced efficiency that the mechanical clam harvesting process known as clam kicking brings to the fisherman who adopts it instead of hand raking. Yet the enhanced efficiency may itself be a danger if the resource is thereby overfished beyond its capacity to sustain harvest. Our data on the negative impacts of clam harvest do not permit one method to be selected in preference to another except to the degree that hand raking might never reach the same harvest intensity and, therefore, might not cause the same magnitude of effects on seagrass beds and their fauna. Outside seagrass beds, clam kicking does not appear to have any serious negative impacts on other parameters of ecological value with the possible exception of hard clam recruitment. This effect is probably a necessary price to pay for the harvest of the adult, marketable clams. Inside seagrass beds, effects of clam kicking on seagrass biomass and bay scallop abundance are quite serious and long-lasting. Because seagrass contributes so substantially to the production of many coastal fisheries (Thayer et al. 1985), any regulation that might limit the intensity of clam fishing in that habitat would probably be beneficial. Restriction of the much more efficient mechanical clam harvesters to unvegetated bottoms may be a suitable mechanism for limiting the total harvest pressure in seagrass beds and, thereby, preserving other fish-

eries in the face of emerging new technology, which has the potential to enhance greatly the user conflicts for limited and interdependent coastal and estuarine resources.

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LITERATURE CITED

ADAMS, S. M.
1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. J. Exp. Mar. Biol. Ecol. 22:269-291.

CADDY, J. F.
1973. Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. J. Fish. Res. Board Can. 30:173-180.

CASTAGNA, M., AND J. N. KRAEUTER.
1977. *Mercenaria* culture using stone aggregate for predator protection. Proc. Nat. Shellfish. Assoc. 67:1-6.

COMMITO, J. A.
1976. Predation, competition, life-history strategies, and the regulation of estuarine soft-bottom community structure. Ph.D. Thesis, Duke Univ., Durham.

CONNELL, J. H., AND W. P. SOUSA.
1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. 121:789-824.

DICKIE, L. M.
1974. Interaction between fishery management and environmental protection. J. Fish. Res. Board Can. 30:2496-2506.

ECKMAN, J. E.
In press. The role of hydrodynamics in recruitment, growth and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. J. Exp. Mar. Biol. Ecol.

FOLK, R. L.
1984. Petrology of sedimentary rocks. Hemphill Publ. Co., Austin.

FONSECA, M. S., J. S. FISHER, J. C. ZIEMAN, AND G. W. THAYER.
1983. Influence of the seagrass *Zostera marina* L. on current flow. Estuarine Coastal Shelf Sci. 15:351-364.

GINSBURG, R. N., AND H. A. LOWENSTAM.
1958. The influence of marine bottom communities on the depositional environment of sediments. J. Geol. 66:310-318.

GRAY, J. S.
1974. Animal-sediment relations. Oceanogr. Mar. Biol. Annu. Rev. 12:223-262.

GROSS, M. G.
1971. Carbon determination. *In* R. E. Carver (editor), Procedures in sedimentary petrology, p. 573-596. Wiley-Interscience, N.Y.

GUTHRIE, J. F., AND C. W. LEWIS.
1982. The clam-kicking fishery of North Carolina. Mar. Fish. Rev. 44(1):16-21.

HECK, K. L., JR., AND R. J. ORTH.
1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay - Decapod Crustacea. Estuaries 3:289-295.

HULBERG, L. W., AND J. S. OLIVER.
1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. Can. J. Fish. Aquat. Sci. 37:1130-1139.

HURLBERT, S. H.
1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187-211.

INGRAM, R. L.
1971. Sieve analysis. *In* R. E. Carver (editor), Procedures in sedimentary petrology, p. 49-94. Wiley-Interscience, N.Y.

KIKUCHI, T.
1966. An ecological study on animal communities of the *Zostera marina* belt in Tomioka Bay, Amakusa, Kyushu. Publ. Amakusa Mar. Biol. Lab. 1:1-106.
1980. Faunal relationships in temperate seagrass beds. *In* R. C. Phillips and C. P. McRoy (editors), Handbook of seagrass biology: an ecosystem perspective, p. 153-172. Garland STPM, N.Y.

KIRBY-SMITH, W. W.
1972. Growth of the bay scallop: the influence of experimental water currents. J. Exp. Mar. Biol. Ecol. 8:7-18.

MCCALL, P. L.
1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35:221-266.

MEADOWS, P. S., AND J. I. CAMPBELL.
1972. Habitat selection by aquatic invertebrates. Adv. Mar. Biol. 10:271-382.

MYERS, A. C.
1977. Sediment processing in a marine subtidal sand bottom community: II. Biological consequences. J. Mar. Res. 35: 633-647.

NELSON, W. G.
1979. An analysis of structural pattern in an eelgrass (*Zostera marina*) amphipod community. J. Exp. Mar. Biol. Ecol. 39:231-264.

ORTH, R. J.
1977. The importance of sediment stability in seagrass communities. *In* B. C. Coull (editor), Ecology of marine benthos, p. 281-300. Univ. South Carolina Press, Columbia.

ORTH, R. J., AND K. L. HECK, JR.
1980. Structural components of eelgrass (*Zostera marina*)

meadows in the lower Chesapeake Bay - Fishes. Estuaries 3:278-288.

PETERSON, C. H.
1982a. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Mar. Biol. 66:159-170.
1982b. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecol. Monogr. 52:437-475.
1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? Am. Nat. 124:127-133.
1985. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: Is pattern fixed during settlement season or altered by subsequent differential survival? Limnol. Oceanogr. 31:200-205.

PETERSON, C. H., H. C. SUMMERSON, AND S. R. FEGLEY.
1983a. Relative efficiency of two clam rakes and their contrasting impacts on seagrass biomass. Fish. Bull., U.S. 81:429-434.

PETERSON, C. H., P. B. DUNCAN, H. C. SUMMERSON, AND G. W. SAFRIT, JR.
1983b. A mark-recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. Fish. Bull., U.S. 81:765-779.

PETERSON, C. H., H. C. SUMMERSON, AND P. B. DUNCAN.
1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. J. Mar. Res. 42:123-138.

REISE, K.
1977. Predation pressure and community structure of an intertidal soft bottom fauna. *In* B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden (editors), Biology of benthic organisms, p. 513-519. Pergamon Press, N.Y.
1978. Experiments on epibenthic predation in the Wadden Sea. Helgol. Wiss. Meeresunters. 31:55-101.

RHOADS, D. C.
1974. Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Annu. Rev. 12:263-300.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191:1-382.

STEWART-OATEN, A., W. W. MURDOCH, AND K. R. PARKER.
1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67:929-940.

STONER, A. W.
1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bull. Mar. Sci. 30:537-551.

SUMMERSON, H. C., AND C. H. PETERSON.
1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Mar. Ecol. Prog. Ser. 15:63-77.

SUTHERLAND, J. P.
1974. Multiple stable points in natural communities. Am. Nat. 108:859-873.

SUTHERLAND, J. P., AND R. H. KARLSON.
1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecol. Monogr. 47:425-446.

THAYER, G. W., D. A. WOLFE, AND R. B. WILLIAMS.
1975. The impact of man on seagrass systems. Am. Sci. 63:288-296.

THAYER, G. W., W. J. KENWORTHY, AND M. S. FONSECA.
1985. The ecology of eelgrass meadows of the Atlantic coast: a community profile. U.S. Fish Wildl. Serv., Wash., D.C. FWS/OBS-84/02, 147 p.

THISTLE, D.
1981. Natural physical disturbances and communities of marine soft bottoms. Mar. Ecol. Prog. Ser. 6:223-228.

WARME, J. E.
1971. Paleoecological aspects of a modern coastal lagoon. Univ. Calif. Publ. Geol. Sci. 87:1-131.

WILLIAMS, J. G.
1980. The influence of adults on the spat of the clam, *Tapes japonica*. J. Mar. Res. 38:729-741.

WILSON, W. H., JR.
1981. Sediment-mediated interactions in a densely populated infaunal assemblage: The effects of the polychaete *Abarenicola pacifica*. J. Mar. Res. 39:735-748.

WOODIN, S. A.
1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. J. Mar. Res. 34:25-41.

ZIEMAN, J. C.
1982. The ecology of the seagrasses of south Florida: a community profile. U.S. Fish Wildl. Serv., Off. Biol. Serv., Wash., D.C. FWS/OBS-82/85, 158 p.

BIOLOGICAL DATA ON BERRY ISLANDS (BAHAMAS) QUEEN CONCHS, *STROMBUS GIGAS*, WITH MARICULTURE AND FISHERIES MANAGEMENT IMPLICATIONS

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ABSTRACT

Biological data designed to assess the mariculture potential of queen conchs, *Strombus gigas*, and to aid in management of stocks in the Berry Islands, Bahamas, were collected from March 1980 to February 1983. Juveniles congregated in shallow areas adjacent to cays with strong currents. Growth of queen conchs differed among cays and seemed related to conch density. Average growth rates from several cays in the Berry Islands showed that growth was slower than that reported for queen conchs in other areas in the Caribbean. Estimated survival of juvenile queen conchs (about 10 cm) was 57-80% per month, or 2-9% annually. Yield per recruit from this population can be maximized by harvesting the animals at about 15 cm, which is the size at onset of lip formation but may be below the size at maturity. Presently, potential for increasing queen conch production through intensive and/or extensive mariculture seems low because of high hatchery costs, lack of dependable mass-rearing techniques, high predation on young released in nature, and slow growth of penned conchs.

The queen conch, *Strombus gigas*, a giant marine snail which is a major food resource in the Caribbean, Bahamas, and some Central American nations, has been exploited by subsistence and commercial fishermen for centuries. During the last several decades, recreational conch fisheries have developed and expanded considerably, placing high fishing pressure on these stocks. Until recently there has been little scientific research directed at improving production from existing stocks. The present study was designed to obtain biological data to fulfill this need in the Berry Islands, Bahamas.

Based on its high fecundity, feeding habits, limited migration habits, and high market demand, queen conch appears to be a desirable candidate for both intensive mariculture (enclosed) and extensive mariculture (released into nature to augment natural stocks) (Berg 1976; Brownell 1977; Brownell et al. 1976; Brownell and Stevely 1981). Success of either type of mariculture is dependent upon technical ability to mass-rear queen conch inexpensively from eggs on a dependable basis, and on knowledge of optimal natural habitats for raising juveniles to a sufficiently large size for either release in nature or for grow-out for market.

Our research on hatchery methods and potential of queen conch mariculture is described in Siddall (1983) and Iversen (1983), and the role of predators in limiting the size of conch populations is described in Jory (1982), Jory and Iversen (1983), and Iversen et al. 1986. Much of the information needed to assess feasibility of increasing queen conch production through mariculture is directly relevant to management of wild stocks. Specific objectives of the Berry Islands field work were to obtain data on age and growth, survival, and optimal habitat for rapid growth and high survival of early life stages. Based on this information, we make recommendations for management of wild stocks.

Our study area, the Berry Islands, lies on the northeastern edge of the Great Bahamas Bank (lat. 25°35′N, long 77°45′W) about 190 km east of Miami, FL (Fig. 1). This area is characterized by small cays, shallow sand flats (2-4 m deep) with abundant turtle grass, *Thalassia testudinium*, beds. The 30 plus islands are located on the west side of the N.E. Providence Channel and north of the Tongue of the Ocean. The islands are generally low-lying and covered with dense undergrowth, Australian pines, and palm trees. Tidal currents, frequently quite strong, set in and out of the openings between cays. Most cays are privately owned and sparsely populated.

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The habitat of the juvenile queen conch in our study area consisted of a large shallow plain surrounded by deep offshore waters. With a few exceptions, large adults were found in these deep areas and channels.

METHODS AND MATERIALS

Collections and observations were made at stations on adjacent cays: Little Whale Cay, Whale Cay, Vigilant Cay, Little Cockroach Cay, Bird Cay, Cat Cay, and Frazer's Hog Cay (Chub Cay) (Fig. 1). Twenty-three field trips were made to the Berry Islands from February 1980 through February 1983, each lasting 4-5 days.

The two methods used to obtain growth estimates were tagging-recapture and size-frequency analysis (Cassie 1954). After trying several different tags for conchs, we found that a thin plastic tag measuring 9.5 × 22.3 mm, obtained from the Floy[3] Tag Co. (Seattle, WA) was satisfactory. It was easily seen and suitable for even the small (ca 2-3 cm) conchs we tagged. A spot on the spire of conchs to be tagged was cleaned and dried, and the tag was affixed with underwater epoxy. We found these tags remained on wild conchs for about 2 years with indications of only a few being shed, of the 2,775 conchs we tagged and released at the sites mentioned above.

For growth estimates we measured queen conchs to the nearest mm along the anterior-posterior axis using a measuring board. Significant differences in growth rates of tagged conchs among cays and size classes were tested by analysis of variance. A Student-Neuman-Keuls test was used to detect significant differences. Differences were considered significant for all statistical tests at the $P = 0.05$ level. Mean values include 95% confidence intervals.

We derived whole animal weight-shell length relationships for queen conchs by measuring whole animal weight after removing conchs from their shells. We then removed everything but the foot to

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

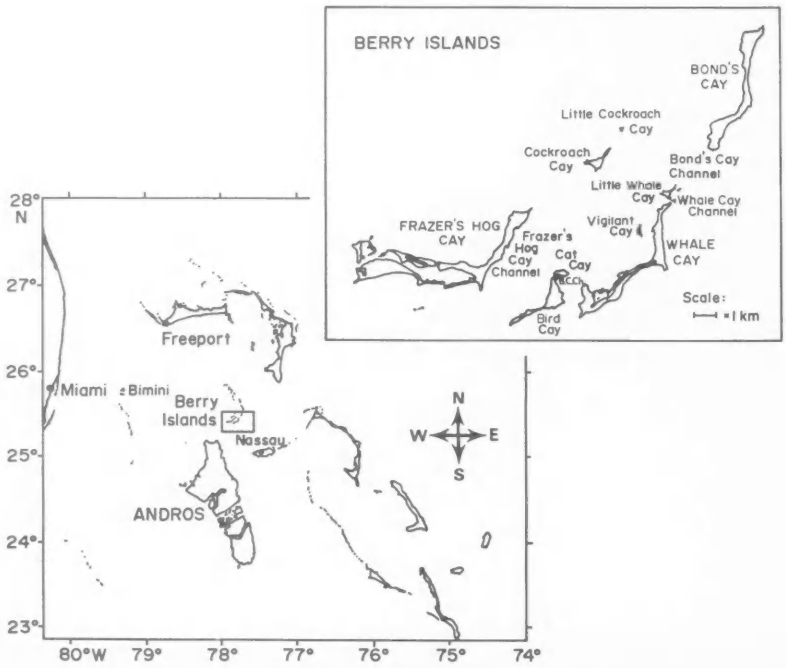


FIGURE 1.—Location of study site.

measure market weight. Significant differences in weight-length and whole animal weight-market weight relationships of conchs among cays were determined by analysis of covariance. Survival rates were obtained from the decrease in numbers of tagged queen conch at each of the tagging sites using Jackson's formula for monthly estimates and Heincke's formula for annual estimates as described in Everhart et al. (1975).

We used pens and cages of varying sizes to evaluate the feasibility of intensive mariculture. Six pens, each 25 m^2, were constructed with walls of monofilament webbing 30 cm high, held up by buoys. Pen walls were held in close contact with the bottom by heavy chains and stakes driven into the bottom, and were stocked with conchs 10-15 cm at densities of 1 or 2 conchs/m^2. Tagged conchs in this size range released in the vicinity of the pens served as controls.

Two additional large pens, 90 and 100 m^2 in area, were planted with 1 conch/m^2, the conch in the size range of 10-15 cm. Various studies on growth and survival in pens ran from 1 to 15 months.

Three wooden floating cages were used to measure growth and survival of small conchs (2-5 cm) over a 1-yr period. They were covered with fine NITEX 4 mm screening and measured 1 × 1 × 0.6 m, stocked with 50 conchs; 0.61 × 0.61 × 0.61 m, stocked with 10 conchs; and 1.6 × 1.2 × 0.6 m, stocked with 100 conchs.

Searches for small, young-of-the-year queen conch (<3 cm) were made by towing a dredge, by sieving sand samples with 4 mm mesh, by towing divers, by walking and digging on tide flats, by towing a shrimp try net (3 m opening and 1.3 cm stretched mesh), and by a suction dredge (Iversen et al. 1986).

To assess density of wild queen conch stocks in shallow water, counts were made along 100 m transects perpendicular and parallel to the shore. All queen conchs lying within 1 m of either side of the transect were counted. Significant differences in density of conchs among cays were tested by analysis of variance.

Most searches for queen conch were made during the day. To determine if this animal's burying activity varied between day and night, we conducted day-night counts at several cays and in our pens, and found no differential burying activity. Previous studies in the Virgin Islands (Randall 1964) and Puerto Rico (Appeldoorn and Ballantine 1983) reported no day-night differences in burying activity.

RESULTS AND DISCUSSION

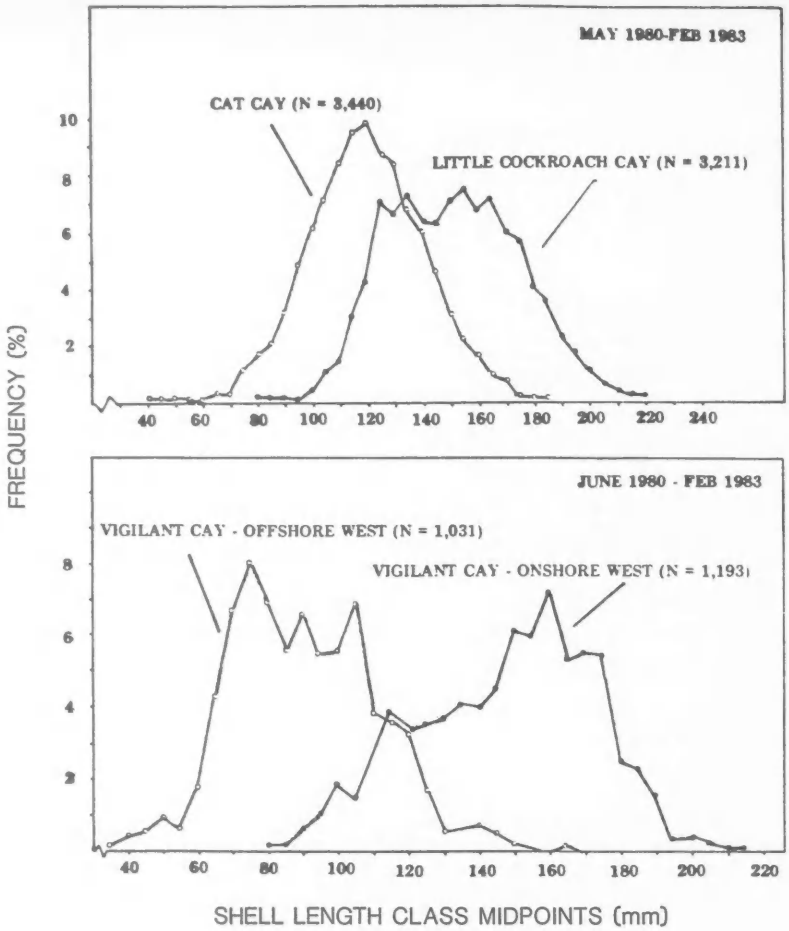
Queen Conch Distribution and Movement

Queen conchs sampled ranged from 2 to 26 cm in length (Fig. 2). The smallest conchs (<10 cm) were found on tidal flats, in shallow waters (<1 m), mostly on sandy bottoms with depressions. The largest juveniles were found in high concentrations near shores of cays, many exposed on low tides. Concentrations of adults with flared lips almost without exception were found in deep water (>3 m). Juveniles were found associated with cays having tidal flats, available food (microalgae and detritus), beaches with a gradual slope, and good water circulation. None was found in the large, open shallow-water areas between cays.

On all 23 field trips, young-of-the-year queen conchs were sought in the course of our regular field activities. The largest concentrations of young were found on the tidal flats between Bird Cay and Cat Cay (Iversen et al. 1986). Lack of shell epibionts on conchs and extensive searching suggested that small queen conchs live in the substrate and in rubble depressions until they are about 0.5 yr old, or about 3-5 cm long, at which time they are found on the tidal flats and nearshore areas in the Berry Islands. Size-frequency distributions (Table 1) showed that smallest individuals spawned the previous year (estimate based on laboratory-reared queen conchs by Siddall [1983], Brownell [1977], and others) appeared in winter, spring, and early summer.

Large juvenile queen conchs (10-18 cm) were easily located on the substrate surface all year long, generally in shallow water. Relatively few lipped queen conchs (N = 109; mean size = 19.3 ± 0.5 cm) were found during the study, most in channels 6 m deep although a few individuals were seen in shallow waters characteristic of most of our study sites. At least one lipped conch was recorded for all areas except Frazer's Hog Cay and Bird Cay-Cat Cay tidal flats. The smallest lipped conchs were found at Cat Cay ($\bar{X}$ = 14.8 ± 2.6 cm; N = 6). Lipped conchs were found every month except February, July, September, and December, with most found in April (N = 46) and October (N = 39). The distribution and seasonal occurrence of lipped conchs may reflect fishing pressure as much as potential reproductive activity.

Studies by Randall (1964), D'Asaro (1965), Brownell (1977), and Weil and Laughlin (1984) indicated that queen conchs have a protracted spawning season as long as March to October. Average length


MAY 1980-FEB 1983
CAT CAY (N = 3,440)
LITTLE COCKROACH CAY (N = 3,211)
FREQUENCY (%)
JUNE 1980 - FEB 1983
VIGILANT CAY - OFFSHORE WEST (N = 1,031)
VIGILANT CAY - ONSHORE WEST (N = 1,193)
SHELL LENGTH CLASS MIDPOINTS (mm)

of lipped conchs reported for the Virgin Islands was 20.4 cm (Randall 1964). Randall noted that lipped conchs sampled in the Berry Islands were smaller in length than conchs taken elsewhere in the Bahamas, or in the Virgin Islands.

Without exception, tagged queen conchs stayed at the cays where they were released, including transplanted queen conchs from nearby cays. It is possible that we did not observe migration because the majority of conchs we sampled were juveniles. Hesse (1979) reported that adult queen conch in Turks and Caicos ranged farthest (about 2 km) from the tagging site and made seasonal migrations offshore in fall and inshore in spring, while juveniles moved <1 km. Weil and Laughlin (1984) reported similar movements for adult and juvenile queen conchs in Venezuela.

Queen Conch Density by Areas

Since the density of queen conch in local areas can affect growth (Alcolado 1976; Weil and Laughlin 1984; Appeldoorn and Sanders 1984), we made density estimates at each of our sampling sites. The mean density of queen conchs at all locations studied, based on 100 m transects taken perpendicular to shore, was $\bar{X} = 7.9 \pm 1.2$ conchs/10 m^2. Highest mean densities were found at Bird Cay

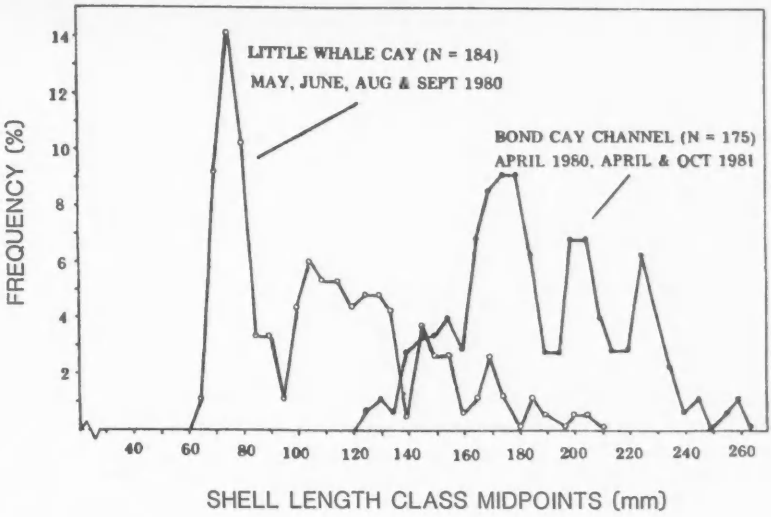

LITTLE WHALE CAY (N = 184)
MAY, JUNE, AUG & SEPT 1980
BOND CAY CHANNEL (N = 175)
APRIL 1980, APRIL & OCT 1981
FREQUENCY (%)
SHELL LENGTH CLASS MIDPOINTS (mm)

FIGURE 2.—Shell length distribution of queen conchs in the Berry Islands.

TABLE 1.—Size-frequency distribution of queen conch at Little Cockroach Cay (May 1980-April 1981).

Length (cm)	1980								1981			
	May	June	July[1]	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.[1]	Mar.	Apr.
8.0-9.0	1										2	
9.0-9.9	1											1
10.0-10.9	7	3						1	6		3	2
11.0-11.9	7	7		2				10	18		16	16
12.0-12.9	31	16		4	1			18	45		54	36
13.0-13.9	32	27		14	5	5	1	8	25		58	34
14.0-14.9	35	25		25	12	11	5	7	12		19	20
15.0-15.9	54	34		32	17	27	17	11	13		16	6
16.0-16.9	66	42		48	24	21	15	7	9		11	5
17.0-17.9	37	34		45	25	36	27	5	4		2	4
18.0-18.9	8	8		35	22	44	36	2	3		4	3
19.0-19.9	3	2		9	19	22	18	2	1		1	2
20.0-20.9				2	3	8	15	3	3		2	2
21.0-21.9				1		3	3		1		1	
Totals	282	198		217	128	177	137	74	140		189	131
Lipped conchs	0	0		1	0	1	3	0	1		0	0

[1]No data.

Channel, $\bar{X}$ = 19.6 ± 2.6 conchs/10 m^2, followed by Vigilant Cay west, $\bar{X}$ = 13.5 ± 3.1 conchs/10 m^2, and Vigilant Cay east, $\bar{X}$ = 12.2 ± 2.9 conchs/10 m^2. Lowest mean densities were found at Little Cockroach Cay, $\bar{X}$ = 1.5 ± 0.7 conchs/10 m^2 and Little Whale Cay north, $\bar{X}$ = 3.3 ± 0.7 conchs/10 m^2 (Table 2).

The mean queen conch density for all locations combined varied between June, September, and November. Density was highest in June ($\bar{X}$ = 9.9 ± 0.3 conchs/10 m^2, N = 978) followed by November ($\bar{X}$ = 6.7 ± 0.4 conchs/10 m^2, N = 673) and September ($\bar{X}$ = 6.0 ± 0.3 conchs/10 m^2; N = 722).

Queen conchs were randomly distributed over the 100 m transect at all locations except Cat Cay and Vigilant Cay, according to the results of a serial ran-

domness test (Zar 1974). Conchs were especially clumped at Cat Cay, all appearing within 10 m of shore, effectively making their densities much higher than were reported for 100 m transects (Table 2).

Queen conch densities reported for other areas in the Caribbean were generally lower, ranging from 0.8-5.2 conchs/10 m^2 in Cuba (Alcolado 1976), 0.01 conchs/10 m^2 in U.S. Virgin Islands (Wood and Olsen 1983), 0.9 conchs/10 m^2 in the Turks and Caicos (Hesse 1979) to 0.1-21 conchs/10 m^2 ($\bar{X}$ = 4.2 conchs/10 m^2) in Los Roques, Venezuela (Weil and Laughlin 1984).

TABLE 2.—Average density of queen conchs by sampling sites.

Sampling site	Average density (conchs/10 m^2 ± 95% C.I.)	N
Little Cockroach Cay	1.5 ± 0.7	88
Little Whale Cay (North)	3.3 ± 0.7	66
Vigilant Cay (West)	13.5 ± 3.1	808
Vigilant Cay (East)	12.2 ± 2.9	733
Bird Cay Channel	19.6 ± 2.6	391
Cat Cay (North)	4.2 ± 1.2	249
Cat Cay (East)	6.2 ± 3.3	372
Whale Cay	6.2 ± 1.7	123

Growth of Queen Conch by Season, Location, and Size

Seasonal Growth

Based on all data collected between February 1980 and June 1982, there was a significant ($P < 0.001$ ANOVA) seasonal difference in mean length of untagged individuals. Queen conchs measured during winter were smaller than those measured during other seasons (Table 3).

Nearly all growth of juvenile queen conchs in our study took place during the warm summer months, May-September. At Cat Cay, for example, mean growth of tagged conchs ranged from 0.44 to 1.63 cm per month during the summer, and from 0.18 to 0.30 cm per month during the remainder of the year. This is consistent with studies by Randall (1964) on queen conch in St. Croix, U.S. Virgin Islands; by Alcolado (1976) in Cuba; and by Appeldoorn (1985) on small juveniles in Puerto Rico. Our small caged conchs (2.4-3.6 cm at tagging), held for 1 year, increased 3.56 cm on the average; 92% of this increase (3.27 cm) took place between April and October.

TABLE 3.—Mean length of untagged queen conchs collected in each season between February 1980 and June 1982.

Season	Months	Mean length (cm)	N
Winter	December January February	11.9 ± [1]1.8	1,432
Spring	March April May	12.9 ± 1.1	3,475
Summer	June July August	12.6 ± 1.2	3,317
Fall	September October November	13.0 ± 1.3	2,943

[1] ± 95% confidence interval.

Growth by Location and Size

To examine the effect of location and size on growth, mean monthly growth of penned and unpenned tagged queen conch was compared within 3 size groups (<9.6 cm, 9.7-15.3 cm, >15.4 cm) by location. Densities of penned conchs (10-20 conchs/10 m^2) were higher than densities of unpenned conchs (2-20 conchs/10 m^2, $\bar{X}$ = 8) measured in the field. In every size class, unpenned conchs grew significantly faster ($P < 0.001$, ANOVA). Among unpenned conchs, there was a significant interaction effect of location and size on mean monthly growth. Large conchs (>15.4 cm) at Little Cockroach Cay, where density was lowest, grew faster than all other sizes. Small conchs (<9.6 cm) grew the next fastest, followed by intermediate-sized conchs (Table 4). Queen conchs at Cat Cay and Vigilant Cay offshore west, where densities were higher, grew slower as

TABLE 4.—Comparison of mean monthly growth rates (cm) for unpenned queen conchs. Underlined locations indicate significant difference in monthly growth between locations as determined by Student-Newman-Keuls test.

Size class	Tagging locations		
9.6 cm	Vigilant Cay Offshore West	Little Whale Cay	Cat Cay
	(0.40) ± [1]0.3 N = 198	(0.48) ± 0.03 N = 13	(0.50) ± 0.04 N = 114
9.6-15.3 cm	Cat Cay	Little Whale Cay	Little Cockroach Cay
	(0.25) ± 0.02 N = 385	(0.40) ± 0.03 N = 186	(0.48) ± 0.02 N = 248
15.3 cm		Little Whale Cay	Little Cockroach Cay
		(0.31) ± 0.07 N = 23	(0.50) ± 0.03 N = 146

[1] 95% confidence interval.

a group than queen conchs at Little Whale Cay and Little Cockroach Cay (Table 4). Alcolado (1976) also reported that queen conchs in Cuba grew slower in areas of high density (5.2 conchs/10 m^2) than in areas of low density (0.08 conchs/10 m^2). Appeldoorn and Sanders (1984) reported similar results in a laboratory experiment on small juvenile conchs.

There was no significant interaction effect between size and location on growth of penned queen conchs. Smallest conchs in cages grew fastest, followed by intermediate-sized conchs (Table 5). There were insufficient data for large penned conchs to estimate their mean monthly growth. Among the intermediate-sized conchs where density was known, mean monthly growth was highest in pens with the lowest density (0.1/10 m^2 compared with 0.2/10 m^2).

Randall's (1964) penned queen conchs (mean length 6.2 and 7.5 cm, range 5.2-8.0 cm; N = 25) grew slowly (0.26 cm/month), but these measurements were made during winter months. Pen size was not specified. In another experiment, Randall placed 16 tagged conchs (19.0-20.0 cm, $\bar{X}$ = 19.4 cm) in a "60 ft by 140 ft elliptical fenced area" during winter and reported average growth of 0.1 cm/month through April when the experiment was discontinued.

Growth rates for our larger penned conchs (mean length 10.3 cm) approximated Randall's rates (0.1 and 0.2 cm/month), even though our data were recorded throughout the year. Growth rates were higher for our smaller conchs (mean length = 4.6 cm; mean growth = 0.4 and 0.2 cm/month) than for larger conchs.

Length at Age

Estimates of length at ages 1-3 were obtained for Berry Islands queen conchs by length-frequency analysis (Cassie 1954) and by fitting the von Bertalanffy equation to tagging data. Distinct length modes of 634 queen conchs measured in October 1980 were present at 7.6, 12.5, and 17.0 cm, suggesting length at ages 1, 2, and 3, respectively.

Parameters in the von Bertalanffy (1938) equation were estimated by fitting a Walford (1946) line to tagging data from Cat Cay, Vigilant Cay, Little Whale Cay, and Little Cockroach Cay (N = 117). Fitting a Walford growth line requires that the growth rate decreases with age. Since the largest queen conchs at Little Cockroach Cay grew faster than the middle-sized juveniles, we excluded these data from our calculations and obtained the following estimates of average length by ages (Table 6).

Age	*Lt (cm)*	
I	8.3	
II	12.2	
III	15.4	
IV	18.1	With L_∞ = 30.0
		K = 0.20
		t_0 = −0.65.

Our estimates of length at age from both length-frequency analyses and von Bertalanffy estimates of tagging data (excluding Little Cockroach Cay data) indicate that queen conch in the Berry Islands grow more slowly than those in the Virgin Islands and some of the areas in Cuba where density was low (0.8 conchs/10 m^2). We suggest that the higher densities of queen conch and cooler water temperatures in the Berry Islands may slow their growth relative to other areas.

Length-Weight Relationship

Whole animal weight(minus the shell)-shell length relationships were derived for queen conch sampled at Chub Cay (N = 39), Frazer's Hog Cay (N = 32), and Bird-Cat Cay Channel (N = 34). Log_{10}

TABLE 5.—Comparison of mean monthly growth rates (cm) for penned queen conch. Underlined locations indicate no significant difference in monthly growth between locations as determined by Student-Newman-Keuls test.

Size class	Tagging location						
9.6 cm	Pen 7		Pen 9	Small Wood Cage		Large Wood Cage	
	(0.04) ± [1]0.07 N = 25		(0.21) ± 0.06 N = 25	(0.24) ± 0.06 N = 38		(0.35) ± 0.06 N = 66	
9.7-15.3 cm	Pen 5	Pen 6	Pen 7	Pen 2	Pen 9	Pen 3	Pen 1
	(−0.05) ± 0.04 N = 38	(−0.01) ± 0.01 N = 38	(0.04) ± 0.02 N = 64	(0.08) ± 0.02 N = 48	(0.11) ± 0.04 N = 56	(0.15) ± 0.03 N = 45	(0.17) ± 0.05 N = 34
15.4 cm	Insufficient data						

[1]95% confidence interval.

TABLE 6.—Estimates of queen conch length (cm) at age from the Caribbean.

Year class	Berry Islands,[1] Bahamas a	Berry Islands,[1] Bahamas b	Puerto Rico[2]	U.S. Virgin Islands St. John[3]	U.S. Virgin Islands St. Thomas[4]	Cuba[5]	Venezuela[6]
I	7.3	8.3	8.8	10.8	9.0	7.9-11.2	7.6
II	12.5	12.2	12.6	17.0	12.6	12.50-18.8	12.8
III	17.0	15.4	18.0	20.5	15.7	15.5-24.3	18.0
IV		18.1				17.4-28.3	
L (cm)		30.3		26.0		20.8-38.3	
K		0.20		0.52		0.287-0.571	
t_0		−0.65		0		−0.12-0.13	
N	634	103	193	104	301	63-284	161

[1]This study - size frequence (a) and von Bertalanffy fit to tagging data (b).
[2]Berg 1976 - size frequency.
[3]Berg 1976 and Brownell et al. 1976 - von Bertalanffy fit to Randall's (1964) tagging data.
[4]Wood and Olsen 1983 - size frequency.
[5]Alcolado 1976 - von Bertalanffy fit to tagging data from 7 locations.
[6]Brownell 1977 - size frequency.

(weight)-Log_{10} (length) relationships best fit the data. Analysis of covariance showed that queen conch at Frazer's Hog Cay and Chub Cay had similar whole animal weight-shell length relationships but that both differed from conchs at Bird-Cat Cay Channel. Therefore, two relationships were developed.

Frazer's Hog-Chub Cay

$$\text{Log}_{10}(\text{whole animal weight}) = -2.40 + 3.57 \times \text{Log}_{10}(\text{shell length})$$

$$r = 0.95 \quad N = 71$$

Bird-Cat Cay Channel

$$\text{Log}_{10}(\text{whole animal weight}) = -1.36 + 2.84 \times \text{Log}_{10}(\text{shell length})$$

$$r = 0.93 \quad N = 34.$$

Mean lengths of queen conch at Frazer's Hog Cay ($\bar{X}$ = 15.6 ± 0.7 cm) and Chub Cay ($\bar{X}$ = 18.6 ± 0.8 cm) were significantly ($P < 0.001$) larger than those at Bird-Cat Cay Channel ($\bar{X}$ = 13.6 ± 0.1 cm). Shell length-whole animal weight relationships changed with size. Smaller conchs ($\bar{X}$ = 13.6 ± 0.1 cm) increased in weight per unit length faster than did larger conchs ($\bar{X}$ = 17.0 ± 0.7 cm).

We found a close linear relationship between whole animal weight and meat weight of Berry Islands queen conch which did not vary among areas:

$$\text{market weight} = 0.65\,(\text{whole animal weight}) + 6.00$$

$$N = 105;\ r = 0.97.$$

The relationship between shell length and animal weight, although significant ($P < 0.001$) was not as close:

$$\text{market weight} = 11.47\,(\text{shell length}) - 50.69$$

$$N = 105;\ r = 0.84.$$

Table 7 gives the numbers of different aged queen conchs in the Berry Islands needed for 1 pound of market meat. Using the whole animal weight-shell length and whole animal weight-market weight relationships developed above and assuming size at lip formation (14.8-19.3 cm) is the size at harvest, 4-10 queen conchs are needed to produce 1 pound of meat (Table 7). In the Berry Islands 6-8 conchs are needed to make 1 pound of market meat, as opposed to 2-3 and 3-4 conchs/pound from other areas in the Bahamas (Berg 1981). The high numbers of queen conchs per pound of market meat from the Berry Islands may be partially explained by their stunted growth.

TABLE 7.—Number of Berry Island queen conch required to make 1 pound of market meat.[1]

Age	von Bertalanffy estimated length at age	Whole animal weight/conch (g)	Market wt (lb)	No. of conchs to make 1 lb of meat
I	8.3	[2]17.8	0.04	26
II	12.2	[2]53.1	0.09	11
III	15.4	[3]73.0	0.12	9
IV	18.1	[3]130	0.20	5
IV[4]	19.3	164	0.25	4

[1]Market meat = (0.65) (whole animal weight − shell weight) + 6.
[2]Shell length (cm) converted to whole animal weight (gm) with Bird-Cat Cay Channel regression log_{10} (weight) = −1.36 + 2.84 log_{10} (shell length).
[3]Shell length (cm) converted to whole animal weight (g) with Frazer's Cay-Chub Cay regression log_{10} (weight) = −2.40 + 3.57 log_{10} (shell length).
[4]Mean size of lipped queen conchs sampled in Berry Islands.

Survival-Mortality

Estimates of monthly and annual survival of unpenned and penned queen conchs in the Berry Islands were derived from tagging studies. The estimates assume that tags are not overlooked, that tags do not fall off or affect survival, that the tagged population is similar to the untagged population in all other respects and that no emigration occurs during the experiments.

Monthly survival rate of unpenned queen conchs ranged from 57 to 80%, depending on location (Table 8). The estimates for Little Cockroach, Vigilant, and Cat Cays are the most reliable, because more conchs were tagged over a longer period of time at these three locations than at others. Annual survival was low for these areas, ranging from 2 to 9%. These proportions result in estimates of total instantaneous mortality rate, Z, from 2.41 to 3.91, considerably higher than those reported by Alcolado (1976) for queen conch in Cuba (annual survival 15-35%, Z from 1.06 to 1.90) or by Wood and Olsen (1983) for recruited queen conch in St. Thomas, U.S. Virgin Islands (Z from 0.22 to 1.80).

Appeldoorn (1985) found mortality of small juvenile queen conchs (<6.4 cm) in Puerto Rico higher at $Z = 8.62$, or an annual survival of 0.02%. In a recent study of large juveniles and adults, Appeldoorn (in press) estimated annual $Z = 2.67$, with M plus emigration = 1.53 and $F = 1.14$. Our survival estimates are probably low because of problems inherent to tagging studies mentioned above.

Survival of penned queen conchs in 4 of our pens was much higher than survival of unpenned animals (Table 8). Monthly survival ranged from 90 to 97% for penned animals, and annual survival ranged from 28 to 73%. However, all conchs died in the 2 deeper water pens. We attribute much of the increased survival rate of queen conch in our best pens to reduced predation, although an undetermined portion of the increase is due to eliminating emigration and the increased probability of finding tagged animals in an enclosure. However, the positive influence of increased survival must be balanced with the slow growth rates of all but the smaller (4.5-8 cm) sizes in pens.

Seasonality of burying, as demonstrated in our penned conch data and by Hesse (1979), using unpenned queen conch, can affect the estimated survival rate because some of the animals cannot be found. Based on our results in pens, the possible error in survival estimate due to burying would probably be relatively small because over about a 1-yr period, a total of 25 out of 200 queen conchs (about 12%) were buried; however, on any single monitoring trip only 1 or 2 individuals were buried.

Causes of Mortality

It is well documented that predation plays a significant role in the survival of queen conchs (Jory 1982; Jory and Iversen 1983; Iversen et al. 1986) and will not be detailed here. After settlement, at all sizes, even flared lipped, thick-shelled adults are subject to predation by large turtles and fishes; however, the rate of predation is significantly higher on the small, thin-shelled juveniles (2-5 cm) and decreases as the animals grow.

Based on our observations, those of our colleagues and reports in the literature, predation, rather than abiotic factors of the environment, or parasites and disease, seem to be the most important causes of queen conch mortality. Hence, stock size after settlement appears to be predator-controlled. This is not an unusual finding when the wide range of species of queen conch predators feeding on all sizes of conch is considered (Randall 1964; Jory and Iversen 1983; Iversen et al. 1986), together with the important role that predation plays in the mortality of many other mollusks (Jory et al. 1984).

TABLE 8.—Survival estimates for Berry Islands queen conchs.

	Unpenned conchs				Little Whale Cay penned conchs					
	Little Cockroach Cay	Vigilant Cay	Cat Cay	Little Whale Cay	Small wooden cage	Large wooden cage	Pen 1	Pen 2	Pen 3[1]	Pen 4
Monthly survival[2]	0.80	0.72	0.80	0.57	0.96	—	0.93	0.97	0.92	0.90
Annual survival[3]	0.02	0.09	0.09	0.02	0.69	0.13	0.36	0.73	0.36	0.28
Number tagged conch released	282	169	418	59	26	15	25	30	50	25
$\bar{X}$ size (cm)	15.0	8.4	11.4	13.0	7.2	7.6	10.5	10.2	10.2	10.5
Range (cm)	8.2-22.3	6.5-11.7	8.1-19.1	8.6-20.6	5.0-8.0	4.5-9.0	8.5-12.0	6.0-12.5	6.0-12.0	8.5-12.5

[1]Only 11 months involved.
[2]Monthly survival estimates made using Jackson's formula.
[3]Annual survival estimates made using Heincke's formula.

Management Implications: Yield per Recruit

Yield-per-recruit analysis, based on our estimate of the von Bertalanffy growth equation and total mortality from tagging, was conducted for the shallow-water queen conch populations in the southern Berry Islands. Yield per recruit was computed from the model given by Beverton and Holt (1957) which assumes that growth rate, susceptibility to capture, and natural mortality remain constant after age of recruitment.

We believe that the combined data from unpenned queen conch in all areas (excluding Little Cockroach Cay) gave us accurate estimates of growth and mortality. We estimated maximum meat weight for Berry Island conchs to be 463 g, based on the shell length to whole animal weight regression from the Frazer's Hog Cay-Chub Cay area, which was the largest sample. Age at recruitment was assumed to be 3 years (corresponding to a length of 15.4 cm). Maximum age of queen conch, based on L_∞ = 30.3 cm and our von Bertalanffy equation, was 11 years.

Using an overall mean annual survival of 7%, Z is 2.66. Estimates of yield per recruit were obtained for a range of values of M between 0.50 and 2.6. F varied between 0.16 and 2.66, by increments of 0.50, and t_0 varied between 1 and 5 years by increments of 1.10 for each level of M. This analysis probably encompassed any value of M and F that actually existed during the study.

At M = 0.50, age liable to capture that maximizes yield in weight per recruit is 3 years, over a range of F from 0.16 to 2.66. Thus, if fishermen take queen conch of approximately 15 cm and larger, they would maximize the yield available from the population. At all values of M above 0.50, results indicate a stage of underfishing because yield in weight per recruit increases over the range of F and decreases with increasing age liable to capture.

The results of yield-per-recruit analyses are limited for several reasons. First, larger, faster growing queen conchs from Little Cockroach Cay were excluded from the analyses; the von Bertalanffy equation did not describe well the growth of conchs from the full data set. Second, the range of sizes in the tagging studies did not accurately reflect the range of sizes in the total queen conch population in the southern Berry Islands. Most data were collected on immature conchs (before lip formation) that were living on shallow flats near islands. While the purpose of analyzing prospects for mariculture were adequately fulfilled by these data, they should not be used for fisheries management because they, for the most part, do not include the larger adults found in deeper channels between cays.

While these data are preliminary, they indicate an important management principle that was also determined for queen conch in the U.S. Virgin Islands by Wood and Olsen (1983); namely, that maximum yield per recruit is obtained at age of first harvest, which is just at onset of lip formation. In the Virgin Islands they found the maximum yield could be obtained by harvest between 3 and 5 years, at an average length of 15.78-19.1 cm. Maximum yield per recruit may occur below onset of maturity, however, since there is some evidence that queen conch may not be reproductively active until some time after lip formation (Wilkins et al., in press).

Mariculture Potential

Queen conch mariculture potential, one objective of this study, was investigated as a possible means to increase conch production in the Bahamas. A hatchery was established at the University of Miami. Techniques were developed for mass-rearing queen conch from egg masses collected in the wild through the larval stages (Siddall 1983). However, because of the high hatchery costs and high mortality associated with planting young mollusks in the wild (Iversen et al 1986; Jory et al. 1986), supplementing natural conch stocks by extensive mariculture does not appear to be economically feasible at this time. We placed juvenile conchs in pens at densities slightly higher than those in nature and found very slow growth, meanwhile experiencing considerable difficulty in physically maintaining the pens. Further, complete mortalities occurred in some pens, which we cannot explain.

Our results suggest that, for the numbers of queen conch required for supplementing natural stocks, the techniques available could probably only be successful in certain well-protected areas. In Bonaire, a degree of success has been reported by Hensen (1983). For intensive mariculture, unless a special area is found with good water exchange, natural food availability, where most predators can be excluded, and large juvenile conchs released, this technique of attempting to enhance production does not appear to have much potential at this time. With additional research, particularly on developing dependable hatchery techniques and cost-efficient means of predator protection, intensive mariculture may some day play a useful role in increasing production.

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LITERATURE CITED

ALCOLADO, P. M.
1976. Crecimiento, variaciones morfologicas de la concha y algunos datos biologicos del cabo, *Strombus gigas*, L. (Mollusca: Mesogastropoda). Acad. Cienc. Cuba, Ser. Oceanol. 34, 36 p.

APPELDOORN, R. S.
1984. The effect of size on mortality of small juvenile conchs (*Strombus gigas* Linne and *S. costatus* Gmelin). J. Shellfish Res. 4(1):37-43.
1985. Growth, mortality and dispersion of juvenile laboratory-reared conchs, *Strombus gigas* and *S. costatus*, released at an offshore site. Bull. Mar. Sci. 37:785-793.
In press. Ontogenetic changes in natural mortality rate of queen conch, *Strombus gigas* (Mollusca: Mesogastropoda). Bull. Mar. Sci.

APPELDOORN, R. S., AND D. L. BALLANTINE.
1983. Field release of cultured queen conch in Puerto Rico: Implications for stock restoration. Proc. Gulf Carib. Fish. Inst. 35:89-98.

APPELDOORN, R. S., AND I. M. SANDERS.
1984. Quantification of the density-growth relation in hatchery-reared juvenile conch (*Strombus gigas* Linne and *S. costatus* Gmelin). J. Shellfish Res. 4(1):63-66.

BERG, C. J., JR.
1976. Growth of the queen conch, *Strombus gigas*, with a discussion of the practicality of its mariculture. Mar. Biol. (Berl.) 34:191-199.
1981. Proceedings Queen Conch Fisheries and Mariculture Meeting. Wallace Groves Aquaculture Foundation, Bahamas, 46 p.

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181-213.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Invest. Minist. Agric. Fish Food (G.B.) Ser. II, 19, 533 p.

BROWNELL, W. N.
1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus*, and *S. pugilis* in Los Roques, Venezuela. Bull. Mar. Sci. 27:668-680.

BROWNELL, W. N., C. J. BERG, JR., AND K. C. HAINES.
1976. Fisheries and aquaculture of the conch, *Strombus gigas*, in the Caribbean. Paper presented to CICAR-II Symposium, Progress in Marine Research in the Caribbean and Adjacent Regions, Caracas, Venezuela, July 12-16, 1976, p. 59-69.

BROWNELL, W. N., AND J. M. STEVELY.
1981. The biology, fisheries and management of the queen conchs, *Strombus gigas*. Mar. Fish. Rev. 43(7):1-12.

CASSIE, R. M.
1954. Some uses of probability paper in the analysis of size frequency distributions. Aust. J. Mar. Freshwater Res. 5:513-522.

D'ASARO, C. N.
1965. Organogenesis, development, and metamorphosis in the queen conch, *Strombus gigas*, with notes on breeding habits. Bull. Mar. Sci. 15:359-416.

EVERHART, W. H., A. W. EIPPER, AND W. D. YOUNGS.
1975. Principals of fishery science. Comstock Publ. Assoc., Cornell Univ. Press, Ithaca, NY, 228 p.

HENSEN, R. R.
1983. Queen conch management and culture in the Netherlands Antilles. Proc. Gulf Carib. Fish. Inst. 35:53-56.

HESSE, K. O.
1979. Movement and migration of the queen conch *Strombus gigas*, in the Turks and Caicos Islands. Bull. Mar. Sci. 29:303-311.

IVERSEN, E. S.
1983. Feasibility of increasing Bahamian conch production by mariculture. Proc. Gulf Carib. Fish. Inst. 35:83-88.

IVERSEN, E. S., D. E. JORY, AND S. P. BANNEROT.
1986. Predation on queen conchs, *Strombus gigas*, in the Bahamas. Bull. Mar. Sci. 39:61-75.

JORY, D. E.
1982. Predation by tulip snails, *Fasciolaria tulipa*, on queen conchs, *Strombus gigas*. M.S. Thesis, Univ. Miami, Coral Gables, FL, 73 p.

JORY, D. E., AND E. S. IVERSEN.
1983. Queen conch predators: not a roadblock to mariculture. Proc. Gulf Carib. Fish. Inst. 35:108-111.
1985. Molluscan mariculture in the greater Caribbean: An overview. Mar. Fish. Rev. 47(4):1-10.

JORY, D. E., M. R. CARRIKER, AND E. S. IVERSEN.
1984. Preventing predation in molluscan aquaculture. J. World Mariculture Soc. 15:421-432.

RANDALL, J. E.
1964. Contribution to the biology of the queen conch, *Strombus gigas*. Bull. Mar. Sci. Gulf Carib. 14:246-295.

SIDDALL, S. E.
1983. Biological and economic outlook for hatchery production of juvenile queen conch. Proc. Gulf Carib. Fish. Inst. 35:46-52.

WALFORD, L. A.
1946. A graphic method of describing the growth of animals. Biol. Bull. (Woods Hole) 90:141-147.

WEIL, E., AND R. G. LAUGHLIN.
1984. Biology, population dynamics, and reproduction of the queen conch *Strombus gigas* Linne in the Archipelago de los Roques National Park. J. Shellfish Res. 4(1):37-43.

WILKINS, R. M., M. H. GOODWIN, AND D. M. REID.
In press. Research applied to conch resource management in St. Kitts/Nevis. Proc. Gulf Carib. Fish. Inst.

WOOD, R. S., AND D. A. OLSEN.
1983. Application of biological knowledge to the management of the Virgin Islands conch fishery. Proc. Gulf Carib. Fish. Inst. 35:112-121.

ZAR, J. H.
1974. Biostatistical Analysis. Prentice-Hall, Inc. Englewood Cliffs, NJ, 620 p.

REVISION OF THE GAMBA PRAWN GENUS *PSEUDARISTEUS*, WITH DESCRIPTION OF TWO NEW SPECIES (CRUSTACEA: DECAPODA: PENAEOIDEA)

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The genus *Pseudaristeus* (family Aristeidae) is widespread in the Indo-West Pacific where five species—*P. crassipes*, *P. gracilis*, *P. kathleenae* n. sp., *P. protensus* n. sp., and *P. sibogae*—have been found at depths between 719 and 1,785 m; another species, *P. speciosus*, occurs in the southwestern Atlantic, where it was taken at 4,847 m. Females of *Pseudaristeus* possess a styliform, long rostrum, 0.70-1.40 as long as the carapace; most males have shorter ones 0.20-0.57, but some have been found in which the rostrum is as long as that of the females. This suggests that in this genus, as in *Aristeus*, at certain stages of the life cycle, males develop a long rostrum. Following a revised definition of the genus, a key to the species, a synonymy, the location of the types, type-locality, and a list of specimens examined are given for each species. Detailed morphological accounts, including intraspecific variation, accompany statements of maximum sizes, and geographic and bathymetric ranges. The description of *P. gracilis* is the first to take into consideration adult material. In discussing relationships, *P. crassipes*, *P. kathleenae*, and *P. protensus*, sympatric off the coast of India, are shown to constitute a rather homogenous group somewhat distantly related to the other very distinctive members of the genus.

The deep-sea "gamba prawns" of the genus *Pseudaristeus* are widely distributed at depths of 719-1,785 m in the Indo-West Pacific—from the Gulf of Aden and off Natal, South Africa to the Philippines—where five (*P. crassipes*, *P. gracilis*, *P. kathleenae* n. sp., *P. protensus* n. sp., *P. sibogae*) of the six species recognized herein are found. The sixth (*P. speciosus*) occurs in the southwestern Atlantic, off northeastern Argentina. It is unlikely that members of the genus occur in the northwestern Atlantic, including the Gulf of Mexico and the Caribbean, where, although intensive collecting have been conducted, no *Pseudaristeus* have been taken.

The large gamba prawns (reaching as much as 47.5 mm carapace length, about 150 mm total length) that occur at shallower depths might, in the not too distant future, make a minor, but highly esteemed, contribution to the commercial catches of penaeoids in certain areas of the Indo-West Pacific, as do members of other deep-sea genera (*Aristaeomorpha*, *Aristeus*, and *Plesiopenaeus*) of the family Aristeidae.

The genus *Pseudaristeus* has been poorly understood largely because the original descriptions of the first three recognized species, *P. speciosus*, *P. gracilis*, and *P. crassipes*, are inadequate for separating them, and the illustrations of the latter two, although well rendered, are of little help. Incomplete descriptions and inadequate illustrations were primarily responsible for subsequent assignment of specimens of two new species described here to *P. crassipes*, which, like them, occurs in the waters off India.

Availability of the rich collections of *Pseudaristeus* made by the U.S. Bureau of Fisheries steamer *Albatross* during the Philippine Expedition, 1907-10, and the loan of critical material from several museums have enabled me to make detailed studies of all six species of the genus. Included in the accounts of each are numerous diagnostic characters which have not been previously recognized in the four described species. One of these characters is the sinuous ventral antennular flagellum found in male *P. gracilis*, which not only allows a ready identification of these animals but constitutes another significant element for the interpretation or a better understanding of the relations of the members of *Pseudaristeus* to those of the closely allied *Aristeus*.

PRESENTATION OF DATA

In the account of the species, most of the terminology used follows that proposed and illustrated by Pérez Farfante (1969, 1977). The anterolateral carina, a unique feature of one member of *Pseudaristeus*, which has not been cited by me previously,

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extends between the gastro-orbital and branchiostegal-hepatic carinae. The names of various parts of the eye, adopted from Young (1956, 1959), were recently employed and illustrated by Pérez Farfante (1985). The measurement of rostrum length (RL) is the linear distance from apex to orbital margin, that of carapace length (CL) is the distance between orbital margin and the midposterior margin of the carapace, and, finally, that of total length (TL) is the distance from the apex of the rostrum to posterior end of the telson. All measurements are made to the nearest 0.5 mm. The petasmata have been described and all but one depicted unfolded; the illustrations were made from stained specimens. Because more than one species have been found in lots reported by various authors under a single name and new species are described herewith from waters from which records have been previously cited, the map is based on only the specimens examined by me. Scales accompanying the illustrations are in millimeters.

Abbreviations of the repositories of the specimens examined during this study are as follows:

BMNH - British Museum (Natural History), London.
MP - Muséum National d'Histoire Naturelle, Paris.
USNM - National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA - Zoologisch Museum, Amsterdam.
ZMB - Zoologisches Museum der Humboldt - Universitat, Berlin.
ZSI - Zoological Survey of India, Calcutta.

GENUS *PSEUDARISTEUS* CROSNIER, 1978

Hemipenaeus Bate 1881:186 [part].
Aristaeus Wood-Mason and Alcock 1891:278 [part].
Aristeus Anderson 1896:91.
Pseudaristeus Crosnier 1978:81 [type species, by original designation, *Aristaeus crassipes* Wood-Mason 1891:281. Gender masculine].

Diagnosis.—Body slender, covered with densely set minute setae. Rostrum long in females and short or long in males; armed with 2 dorsal teeth; epigastric tooth distinctly posterior to first rostral, situated about 0.1 CL from orbital margin. Antennal and branchiostegal spines present; orbital, pterygostomian, and hepatic spines lacking. Cervical sulcus crossing postrostral carina (rarely only reaching it); postcervical sulcus extending to postrostral carina; gastro-orbital, antennal, branchiostegal-hepatic, and branchiocardiac carinae strong; hepatic sulcus long, usually fusing with branchiocardiac sulcus and descending obliquely almost to margin of branchiostegite. Abdomen with dorsomedian carina extending from fourth through sixth somites; elongate sixth somite bearing pair of long cicatrices. Telson produced posteriorly in sharp, median spine and with posterior 0.4 of length armed with 4 pairs of small, movable, lateral spines. Eye with well-developed cornea and dorsoventrally depressed peduncle bearing mesial tubercle; basal article not produced in scale. Antennular peduncle length about 0.55 CL; prosartema rudimentary, consisting of short stump bearing brush of long setae; dorsal flagellum short, about 0.4 length of antennular peduncle, and flattened; ventral flagellum long, no less than 2.75 CL, and filiform. Mandibular palp (Fig. 1*A*) reaching to about base of ischiocerite (third article of antennal peduncle), distal article suboval and much smaller than basal. Palp of first maxilla unsegmented (Fig. 1*B*). Second maxilla and first and second maxillipeds as illustrated (Fig. 1*C-E*). Exopods on all maxillipeds but lacking on pereopods. Petasma with dorsomedian lobule short, only about 0.4 length of petasma; ventromedian lobule with rib narrow proximally, broadening to level of distal end of dorsomedian lobule where reaching mesial margin, and continuing almost to end of lobule; ventral costa distally free, not attached to dorsolateral lobule; endopod of second pleopod bearing appendices masculina and interna. Thelycum of "open type", with large, lanceolate median plate on sternite XIII. Well-developed podobranchia on second and third maxillipeds and first and second pereopods, those on pereopods subequal in size. One arthrobranchia on somite VII and two on VIII through XIII, all well developed except very small anterior one on somite VIII. Pleurobranchia on somites IX through XIV, that on XIV well developed, remaining ones much smaller. Nonbifurcate, large epipod on somites VII through XII, that on XII subequal in size to that on XI. (Modified from Crosnier 1978.)

It seems worth emphasizing that although the rostrum is long in females, 0.70-1.40 CL, and relatively short in most of the males examined, 0.20-0.57 CL, I have found one male in each of two species with long rostra, 0.70 and 1.40 CL.

Five species known from the Indo-West Pacific are *P. crassipes*, *P. gracilis*, *P. kathleenae* n. sp., *P. protensus* n. sp., and *P. sibogae*; and the one from the southwestern Atlantic is *P. speciosus*. The species from the Indo-West Pacific nave been taken at depths between 750 and 1,785 m and that from the southwestern Atlantic at 4,847 m. These depths and all others cited are those noted for the stations

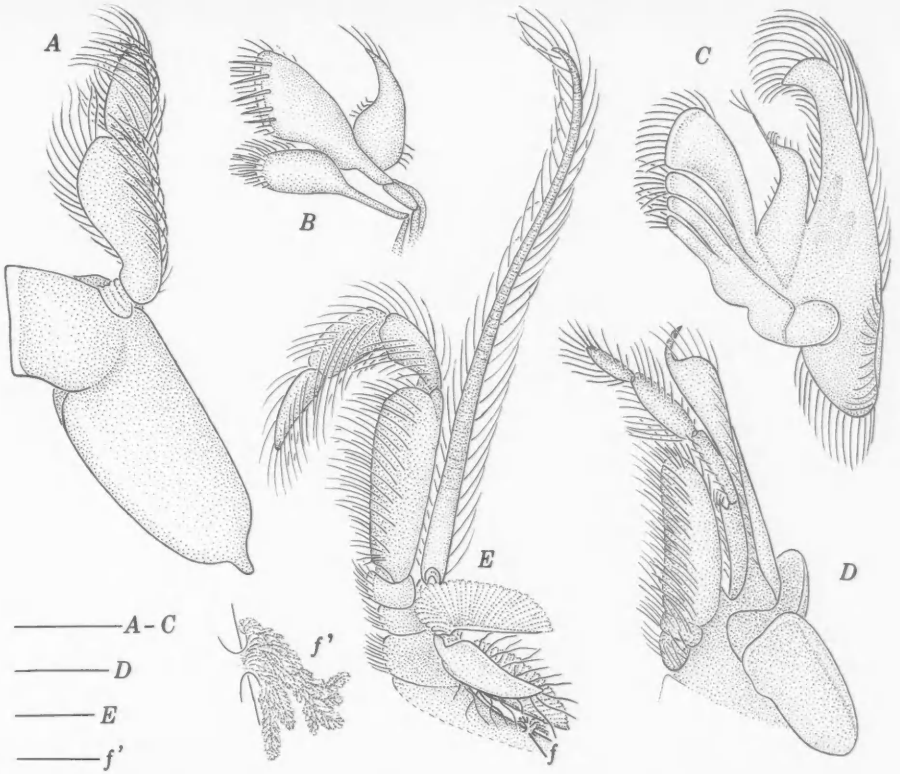


FIGURE 1.—*Pseudaristeus kathleenae* n. sp., ♀ 35 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *D*, First maxilliped. *E*, Second maxilliped. *f*, Rudimentary arthrobranchia. *f'*, Enlargement of *f*. (All from left side). Scales: *A-E* = 3 mm; *f'* = 1 mm.

at which the specimens were obtained, but because open nets were used in collecting, it is not possible to ascertain the actual level at which the shrimp entered the net.

Pseudaristeus is quite close to *Aristeus*, having the same branchial formula, but differing from it in exhibiting a well-marked cervical sulcus which reaches the dorsomedian carina of the carapace and in possessing a postcervical sulcus. Among the members of *Pseudaristeus* only males of *P. gracilis* exhibit a sinuous ventral antennular flagellum, a feature characteristic of the males of all species of the genus *Aristeus*. This similarity, together with a branchial formula common to the two genera, indicates a close affinity between members of the genera *Pseudaristeus* and *Aristeus* and is a convincing basis for the postulate that they have had a more recent common ancestor than either share with *Hemipenaeus*. The species now assigned to *Pseudaristeus* were placed in the genus *Hemipenaeus* by almost all authors in this century until Crosnier (1978) proposed that they be removed to his new genus.

Key to species of *Pseudaristeus*

1. Ventral extremity of cervical carina blunt, not forming sharp-edged arc. Anterolateral carina present. Posterior part of hepatic sulcus not fusing with branchiocardiac sulcus but extending longitudinally subparallel to latter. ..... *P. speciosus*

   Ventral extremity of cervical carina forming

sharp-edged arc. Anterolateral carina absent. Posterior part of hepatic sulcus fusing with branchiocardiac sulcus and continuing posteroventrally oblique to latter. 2

2. Optic calathus long, mesial margin at least 1.5 width of distal extremity. Pereopods covered with minute setae. . . . . *P. sibogae*

Optic calathus short or relatively so, mesial margin 1.3 or less width of distal extremity. Pereopods not covered with setae. 3

3. Thelycum with median plate of sternite XIII very long (length more than 4 times basal width), almost reaching spine on sternite XII, and narrow, maximum width 0.40 length. [Males unknown]. . . . . *P. protensus*

Thelycum with median plate of sternite XIII relatively short (length less than 3.5 times basal width) and broad or relatively broad, maximum width more than 0.40 length. . . . 4

4. Third article of antennular peduncle expanded laterally, forming strong, subtriangular projection in males and variably developed rounded prominence in females. Petasma with ventral costa neither strongly inclined distomesially nor contracted preapically. Thelycum with median plate of sternite XIII moderately broad (maximum width 0.65-0.75 length) and lacking posterolateral prominences. . . . . *P. kathleenae*

Third article of antennular peduncle not expanded laterally, forming neither strong prominence in males nor rounded prominence in females. Petasma with ventral costa strongly inclined distomesially or contracted preapically. Thelycum with median plate of sternite XIII either relatively narrow (maximum width 0.45-0.55 length) or, if broad (0.80-0.93), bearing posterolateral prominances. 5

5. Males with ventral antennular flagellum sinuous proximally and bearing narrow band of densely set small setae distal to dorsal flagellum; petasma with ventral costa markedly contracted preapically. Females with median plate of sternite XIII expanded in pair of conspicuous posterolateral prominences. . . . . *P. gracilis*

Males with ventral antennular flagellum straight proximally and lacking band of small setae; petasma with ventral costa not markedly contracted preapically. Females with median plate of sternite XIII lacking posterolateral prominences. . . . . *P. crassipes*

Pseudaristeus kathleenae, new species

Figures 1-3, 4*C*, 5-9

Aristaeus crassipes. Alcock 1901a:50 [part].
Hemipenaeus crassipes. De Man 1911:24. Kemp and Seymour Sewell 1912:17 [part], pl. 1, fig. 8. De Man 1913, pl. 2, fig. 4*a-c* and in legend to fig. 5 [under Remarks for *H. sibogae*]. Balss 1925:229 [part].

Materials.

Holotype: ♂, USNM 216710, 23.5 mm CL, 6.5 mm RL, about 88 mm TL; type-locality: Teluk Bone, Sulawesi (Celebes), Indonesia; 3°19′40″S, 120°36′30″E; 900 m; gray mud; 19 December 1909; *Albatross* stn 5657.

Paratypes: India—1 ♀, USNM 216711, collected with holotype. 1♂, ZSI 7806/10, W of Cape Comorin, Tamil Nādu, India; 7°46′N, 76°37′E; 1,225 m; 26 April 1911; *Investigator* stn 388. 2 ♂, ZSI, S of Cape Comorin, Tamil Nādu, India; 7°36′N, 78°05′E; 556-595 m; 10 April 1900; *Investigator* stn 268.

Indonesia—1 ♀, ZMB, off W Sumatra; 0°39′S, 98°52′E; 750 m; 31 January 1899; *Valdivia* stn 191. 1 ♂, ZMA, eastern Flores Sea; 7°24′00″S, 118°15′12″E; 794 m; fine gray mud, with some radiolariae and diatomes; 6 April 1899; *Siboga* stn 45. 1 ♀, USNM, Teluk Bone, Sulawesi (Celebes); 3°17′40″S, 120°36′45″E; 885 m; gray mud; 19 December 1909; *Albatross* stn 5656. 3 ♀, USNM, Teluk Bone, Sulawesi (Celebes); 3°32′40″S, 120°31′30″E; 933 m; gray mud; 19 December 1909; *Albatross* stn 5658. 1 ♀, USNM, W of Halmahera; 0°35′00″N, 127°14′40″N, 127°14′40″E; 795 m; fine gray sand, mud; 27 November 1909; *Albatross* stn 5619.

Philippines—2 ♀, USNM, Cagayan Is, Sulu Sea; 9°38′30″N, 121°11′00″E; 929 m; gray mud, coral sand; 31 March 1909; *Albatross* stn 5423. 1 ♂ 1 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°32′30″N, 123°58′06″E; 1,033 m; gray mud; 10 June 1909; *Albatross* stn 5460. 1 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°40′57″N, 123°57′45″E; (549 m); sand; 16 June 1909; *Albatross*

stn 5463. 1 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°39′42″N, 123°40′39″E; 914 m; gray mud; 17 June 1909; *Albatross* stn 5465. 1 ♀, USNM, Verde Island Passage, N of Mindoro; 13°36′11″N, 120°45′26″E; 622 m; fine sand; 20 January 1908; *Albatross* stn 5114. 4 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°35′27″N, 123°37′18″E; 878 m; gray mud; 18 June 1909; *Albatross* stn 5467. 2 ♂ 5 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°36′48″N, 123°38′24″E; 914 m; green mud; 18 June 1909; *Albatross* stn 5469.

Diagnosis.—Optic calathus relatively short, mesial margin 1.0-1.3 times distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle expanded laterally, forming large subtriangular projection in males, but weak to rounded prominence in females; males with ventral antennular flagellum never sinuous, and ultimate article of third maxilliped strongly curved, spatulate and bearing patch of strong, rigid setae. Pereopods not covered with minute setae. Petasma with ventral costa only slightly inclined distomesially, and ventral surface of dorsolateral lobule lacking setae. Thelycum with plate of sternite XIV rather long and produced at either side in short anterolateral hood; median plate of sternite XIII moderately long (not nearly reaching spine on sternite XII), rather broad (maximum width 0.65-0.75 length) but not expanded posterolaterally in conspicuous prominences.

Description.—Body slender (Fig. 2), densely studded with minute setae. Rostrum in males usually short, its length 0.25-0.45 CL (but in one male, 24 mm CL, 1.4 CL), and roughly lanceolate; in females long (Fig. 3), 1-1.15 CL (but in one female 23 mm CL, 0.70 CL), relatively deep and convex basally, styliform and slightly unturned anteriorly. Rostral plus epigastric teeth 3; rostral teeth situated variably in males, basally in females. Adrostral carina strong, in males almost reaching apex, in females (and in male with long rostrum) extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine as long as or longer than antennal and acutely pointed. Cervical sulcus crossing postrostral carina (rarely only reaching it) at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt except for sharp strongly arched ventral extremity; weak postcervical sulcus reaching, but not crossing, postrostral carina at about 0.70 CL from orbital margin. Postrostral carina, extending 0.75-0.80 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina well defined; antennal carina rather short; branchiostegal-hepatic carina long, raised and sharp. Orbitoantennal sulcus shallow; hepatic sulcus fusing with branchiocardiac sulcus, then turning obliquely almost ventrad, forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by carina, long, extending posteriorly to near margin of carapace; blunt, dorsally concave ridge (disposed dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by weak groove, latter approaching cervical sulcus anteriorly and ending about level of postcervical sulcus posteriorly.

Eye (Fig. 4*C*) with optic calathus relatively short, length of mesial margin 1.0-1.3 times distal width; mesial tubercle strong and situated between distal 0.25 and 0.30 length of margin.

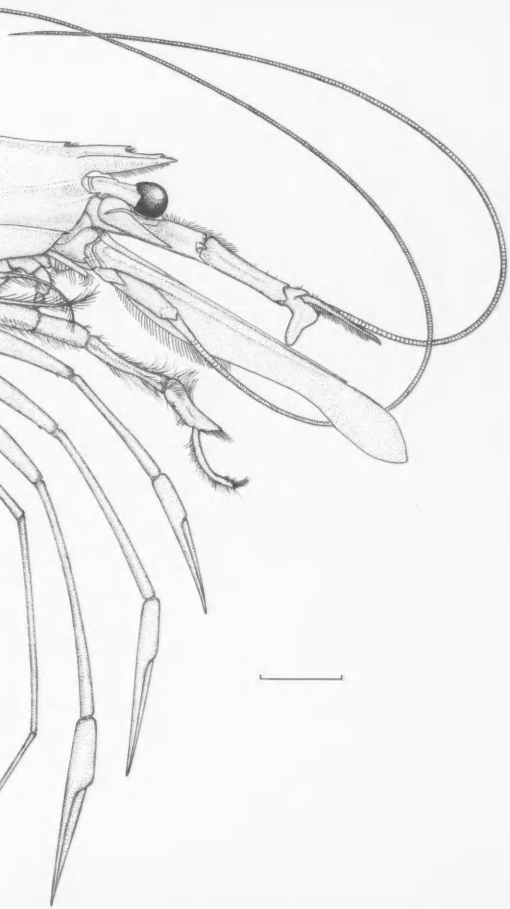
Gnathal appendages, except third maxilliped, illustrated in Figure 1.

Antennular peduncle with stylocerite produced in sharp spine falling conspicuously short of mesial base of distolateral spine; latter small and sharp; third article in adult males uniquely produced in large subtriangular or ax-head shaped projection (Fig. 2) directed ventrolaterally, in females (Fig. 5*B*) expanded laterally in broadly rounded prominence. Dorsal flagellum reaching between distal 0.20 and 0.15 of scaphocerite; ventral flagellum straight and long, although incomplete in all specimens examined, in one male with 19 mm CL its length at least 2.75 times CL.

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum at least 1.25 times TL of shrimp.

Third maxilliped sexually dimorphic. In males (Fig. 5*A*) with penultimate article often slightly to strongly inflated proximally, compressed and produced in strong, subelliptical or acuminate process (overhanging proximal part of ultimate article) distally; article also bearing brush of long thickly set setae on both mesial and lateral surfaces, and dense row of setae along distal margin of process. Ultimate article subspatulate, strongly arched, not expanded basally, bearing distally dense patch of strong, rigid setae on lateral surface, proximalmost setae short and more distal ones considerably longer; terminal margin with tuft of very long flex-

FIGURE 2.—*Pseudaristeus kathleenae*, holotype ♂ 23.5 mm CL, Teluk Bone, Sulawesi



lawesi (Celebes), Indonesia. Lateral view. Scale = 6 mm.

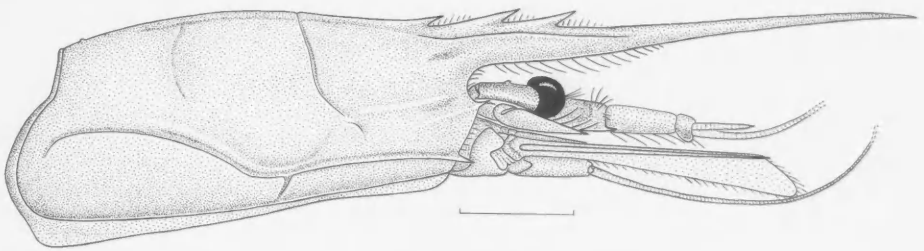


FIGURE 3.—*Pseudaristeus kathleenae*, ♀ 37 mm CL, Verde Island Passage, north of Mindoro, Philippines. Anterior region, lateral view. Scale = 10 mm.

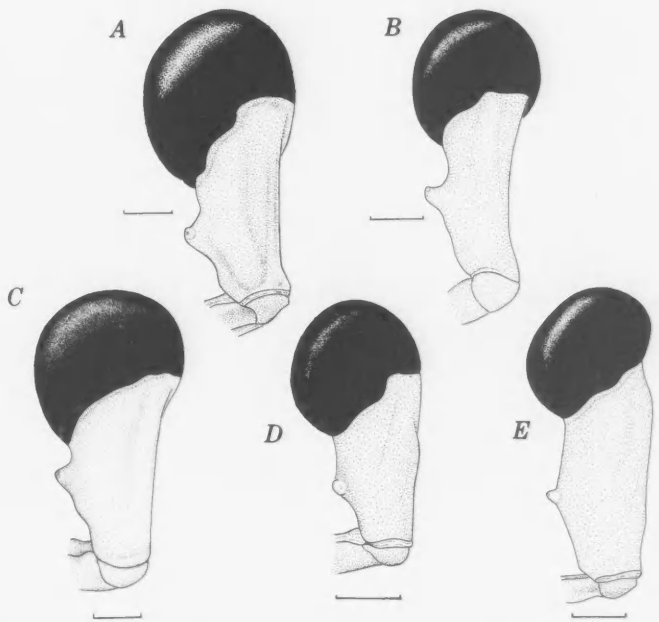


FIGURE 4.—Eyes. *A*, *Pseudaristeus crassipes*, ♂ 28.5 mm CL, south of Cape Comorin, Tamil Nādu, India. *B*, *P. gracilis*, ♂ 20 mm CL, eastern Mindanao Sea, Philippines. *C*, *P. kathleenae*, holotype ♂ 23.5 mm CL, Teluk Bone, Sulawesi, Indonesia. *D*, *P. protensus*, holotype ♀ 40 mm CL, west of Evēral Gujārat, India. *E*, *P. sibogae*, ♀ 47.5 mm CL, south of Pulau Muna, Sulawesi, Indonesia. Scales: *A*, *B*, *C* = 1 mm; *D*, *E* = 2 mm.

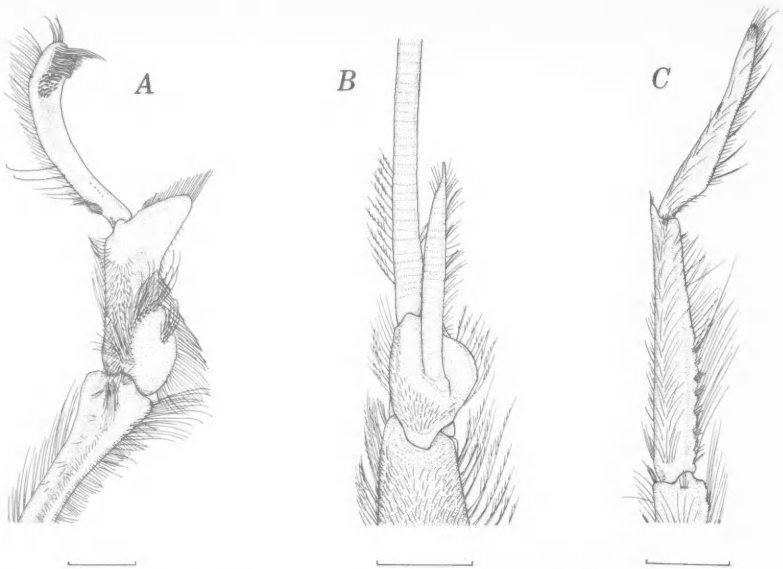


FIGURE 5.—*Pseudaristeus kathleenae*: *A*, ♂ 26 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines, distal articles of left third maxilliped, lateral view. *B*, ♀ 39 mm CL, Teluk Bone, Sulawesi, Indonesia, distal articles of right antennular peduncle and flagella, dorsal view. *C*, same ♀, distal articles of left third maxilliped, dorsal view. Scales = 2 mm.

ible setae, and entire ventral margin supporting numerous ones. In females (Fig. 5*C*), ultimate article slender, flattened, broadening slightly from narrow base, then tapering gently to blunt apex.

Pereopods not covered with setae; first and second with broad, compressed merus bearing small, slender, distomesial spine.

Abdomen with sharp dorsomedian carina extending from posterior 0.75 of fourth somite posteriorly through sixth somite and produced in spine on caudal margin of last 3 somites; sixth also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus weak, usually distinct along anterior 0.75 length of telson, and flanked by paired longitudinal dorsolateral ridges; bearing 4 pairs of movable spines: 3 at about 0.60, 0.75, 0.85 length from basal margin of telson, fourth flanking short terminal part. Mesial ramus of uropod surpassing apex of telson by as much as 0.40 its own length; lateral ramus overreaching mesial ramus by as much as 0.33 its own length.

Petasma (Figs. 6, 7*A*, *B*) with dorsomedian lobule cincinnulate along entire mesial margin. Ventromedian lobule extending distally as far as dorsolateral lobule and bearing elongate, lapel-like flap

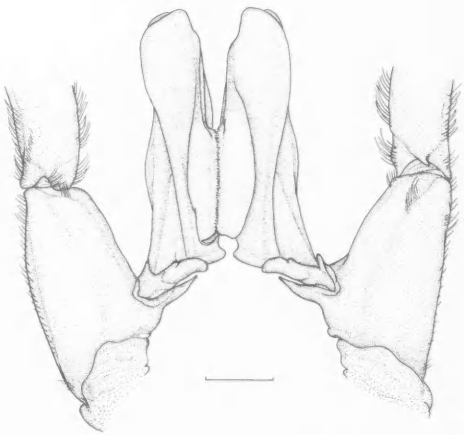


FIGURE 6.—*Pseudaristeus kathleenae*, ♂ 24.5 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines. Petasma and proximal part of first pleopods, dorsal view. Scale = 2 mm.

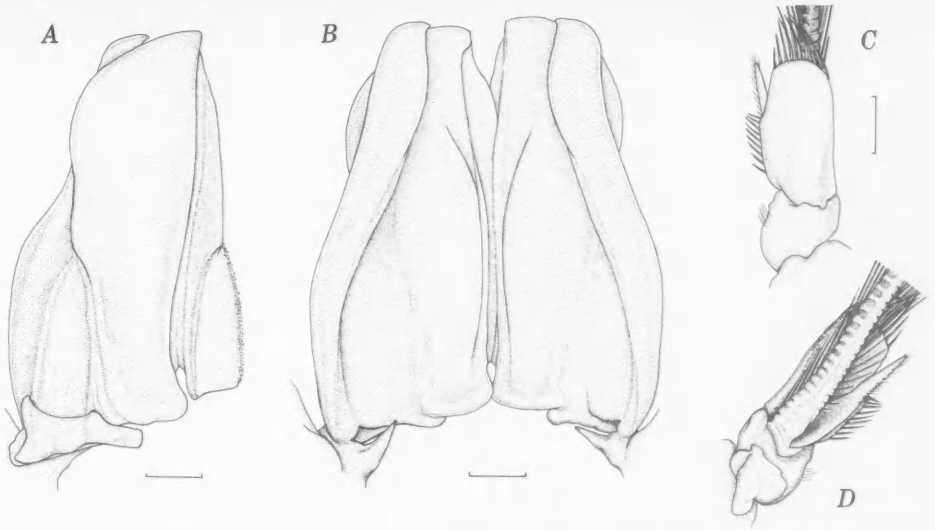


FIGURE 7.—*Pseudaristeus kathleenae*, holotype ♂, 23.5 mm CL, Teluk Bone, Sulawesi, Indonesia. *A*, Petasma, dorsolateral view of left half. *B*, Ventral view. *C*, Right appendices masculina and interna, and basal sclerite of endopod, dorsal view. *D*, Ventral view. Scales = 1 mm.

distoventrally along mesial margin. Dorsolateral lobule sclerotized, expanding distolaterally before tapering to subangulate mesial apex, its distolateral margin strongly curved; ventral surface, exhibiting arched slender rib, lacking setae. Ventral costa gently sinuous, only slightly inclined distomesially, its terminal part forming truncate blade lying free but against ventral surface of dorsolateral lobule.

Appendix masculina (Fig. 7*C*, *D*) roughly obovate, with proximal part curving ventrally embracing appendix interna; its distal margin bearing long setae and mesial margin bearing short, more numerous ones. Appendix interna roughly triangular and subequal in length to appendix masculina.

In males, sternite XIV with setose anteromedian tubercle; plate of sternite XIII elongate (length 2-3 times basal width), broadly rounded anteriorly and produced in minute apical spine bearing tuft of long setae.

Thelycum (Fig. 8) with setose, moderately long plate of sternite XIV either traversed by shallow groove posteriorly or broadly depressed, and with anteromedian margin varying from distinctly concave to slightly convex, plate produced at either side in short anterolateral hood; fossa immediately anterior to plate very conspicuous and bearing pair of small oblique ridges. Median plate of sternite XIII,

FIGURE 8.—*Pseudaristeus kathleenae*, ♀ 47 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines. Thelycum. Scale = 2 mm.

also covered with setae, moderately long (length 3-3.5 times basal width), falling considerably short of spine on sternite XII, broadly lanceolate (maximum width 0.65-0.75 length), and flat or slightly excavate; posterolateral margins of plate, sometimes turned ventrally, abutting slender ridges extending posteromesially before curving laterally on margin of sternite XIII. Sternite XII minutely setose, bearing median keel ending anteriorly in anteroventrally directed sharp spine.

Maximum lengths.—Males, 24 mm CL; females, 46.5 mm CL.

Geographic and bathymetric ranges.—From west of Cape Comorin, India, through Indonesia, and northward to east of Luzon, Philippines (Fig. 9). It has been obtained at depths between 549 and 1,225 m.

Discussion.—This species differs from *P. crassipes*, with which it has been confused previously, in the following unique characteristics. In males, the third article of the antennular peduncle is strikingly produced in a subtriangular or roughly ax-head shaped lateral projection, and in females it is expanded laterally in a broadly rounded prominence. This is a feature by which the females of *P. kathleenae* can be infallibly distinguished from those of *P. crassipes* which, otherwise, are quite similar. In *P. crassipes*, the third article of the antennular peduncle of both sexes is uniform in width proximally and gradually tapers distomesially. In males of *P. kathleenae*, the penultimate article of the third maxilliped is compressed distally and produced in a strong subelliptical or acuminate process which overhangs the ultimate article; the latter is subspatulate, conspicuously curved throughout, almost uniform in width, and bears long rigid setae on the lateral surface. In the males of *P. crassipes* the penultimate article of the third maxilliped is subtriangular in cross section throughout and does not project distally in a conspicuous process but instead is rounded distally; the ultimate article is twisted, expanded basally, and weakly to conspicuously so distally, and bears lateral rows of spinules on its ventral surface.

Pseudaristeus kathleenae differs further from *P. crassipes* in features of the petasma. In the former, the dorsolateral lobule is expanded distolaterally before tapering to a subangulate mesial apex; also the ventral costa is sinuous and does not turn strongly distomesially from its basal part. In contrast, the dorsolateral lobule is not expanded distolaterally in *P. crassipes*, tapers to broadly elliptical apex, and the ventral costa is almost straight basally before turning rather abruptly distomesially. Finally, in females of *P. kathleenae* the median plate of sternite XIII is broader than that in *P. crassipes*, its maximum width ranging from 0.67 to 0.75 rather than from 0.45 to 0.55 as it does in the latter.

In females of *Pseudaristeus* the rostrum is long, almost as long or considerably longer than the carapace, whereas, in males it is usually short, less than 0.33 the length of the carapace. Among the 8 males of *P. kathleenae* examined in this study, one possesses a rostrum that is 1.4 times the length of the carapace (longer than that of any female examined), and among the three available males of *P. crassipes*, the rostrum of one, although proportionally not so long, is 0.7 as long as the carapace. Perhaps these males with long rostra are not as rare as one might anticipate. This suggestion is based on a study by Burukovsky and Romensky (1972) in which they noted considerable variation in the length of the rostrum in another aristeid, *Aristeus varidens*, occurring in the eastern Atlantic from Ghana to Angola. It was well known that in all genera of Aristeidae the rostrum of females is much longer than that of males; however, they found that although the majority of males of this gamba prawn have a relatively short rostrum, in almost 30% of them it is long. Also, they noted that in both sexes the rostrum decreases proportionately with increasing size (a fact well established for penaeoid species) and that this age-dependent variation is different for the sexes: in small females the rostrum may exceed 1.5 times the length of the carapace, whereas in large ones it is about as long as the carapace; in small males the length of the rostrum may be almost 1.5 times that of the carapace, but as they grow it decreases to 0.1-0.5 times. Nevertheless, in individuals of the same size they found that the range of variation is smaller in females than in males. Their study demonstrates that sexual dimorphism in the length of the rostrum, thought to be typical of aristeids, disappears at least in small males of *A. varidens*. This too might obtain in members of *Pseudaristeus*, but because of the lack or paucity of males of all 6 species I am unable to conduct a meaningful investigation of variations in RL/CL. Because no correlation was observed between variations in the length of the rostrum and changes in the petasma or in the structure of the gonads in males with short and long rostrum which would indicate sexual change, Burukovsky and Romensky suggested that the reduction of the rostrum, more marked in males than in females, might be associated with the transition from a benthic to a bathypelagic existence undergone by members of the family Aristeidae.

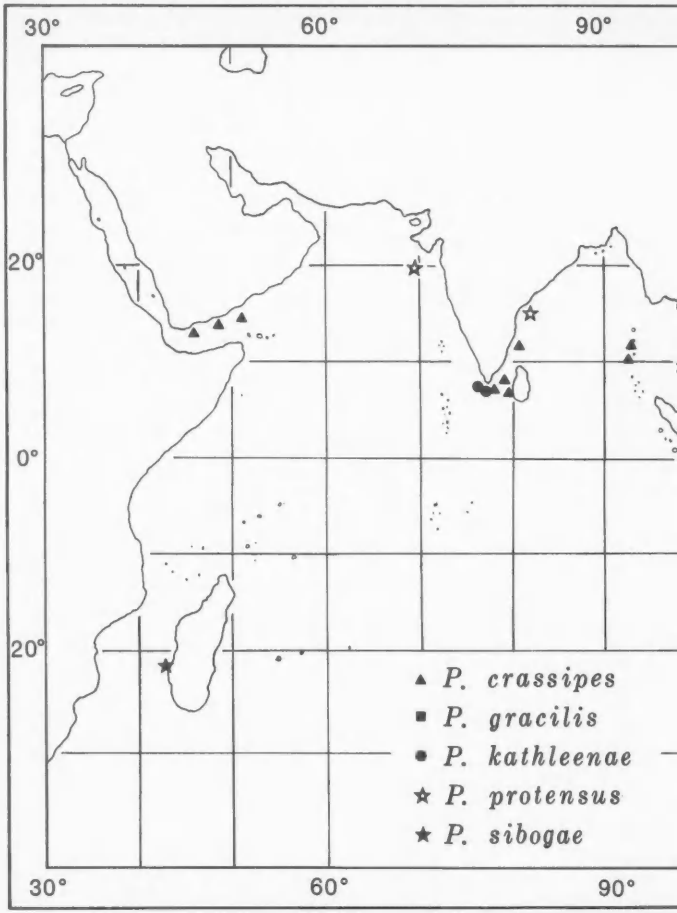
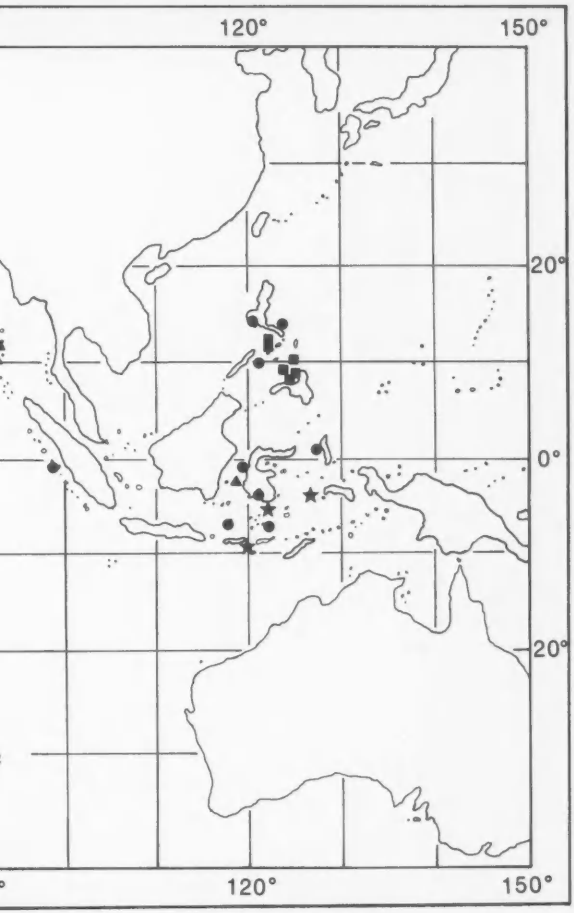


FIGURE 9.—Ranges of *Pseudaristeus crassipes*, *P. gracilis*, *P*



cilis, *P. kathleenae*, *P. protensus*, and *P. sibogae*.

Only a few of the available specimens of this species still have entire pereopods, and even fewer have retained all 5 pereopods; in almost all, the fourth and fifth are missing, or only two or three podomeres are represented. The data obtained by me, however, seem to confirm those presented by De Man (1911) and Crosnier (1978), which indicate that the pereopods of *P. kathleenae* are more slender than those of *P. sibogae*. Their data were based on a female 31 mm CL collected by the Siboga Expedition and identified by them as "*crassipes*". This specimen was examined during the present study and is assigned herein to *P. kathleenae*.

Etymology.—I take pleasure in naming this shrimp for my daughter Kathleen P. Canet.

Pseudaristeus crassipes (Wood-Mason 1891)

Figures 4*A*, 9-13

Aristaeus crassipes Wood-Mason 1891:281, fig. 7 [syntypes: 1 ♀, ZSI 6713/9, Andaman Sea; 11°25′05″N, 92°47′06″E; 405 fm (741 m); green mud; 9 December 1890; *Investigator* stn 116. 1 ♀, ZSI 3171/9 (could not be located in ZSI, 24 November 1984, Maya Deb of ZSI, pers. commun.[2]); off SW Sri Lanka; 6°29′00″N, 79°34′00″E; 597 fm (1,092 m)]. Alcock and Anderson 1894: 147. Faxon 1895:198. Anderson 1896:91. Alcock 1901a:50 [part]; 1902:268, figs. 63, 64a, b.

[?]*Aristaeus crassipes*. Alcock 1898:74. Alcock and Anderson 1899:3. Doflein 1906:259.

Aristaeus (*Hemipeneus*) *crassipes*. Alcock 1901b:33.

Aristeus (*Hemipeneus*) *crassipes*. Alcock and McArdle 1901, pl. 49, figs. 1, 2.

Aristeus crassipes. Lloyd 1907:2.

Hemipeneus crassipes. Kemp and Sewell 1912:17 [part], pl. 1, fig. 9.

Hemipenaeus crassipes. Balss 1925:224 [part]. Ramadan 1938:49. Anderson and Lindner 1945: 301. Ramadan 1952:15, fig. 18. Sewell 1955:203. Burukovsky 1974:48. Silas and Muthu 1979:78. Not *Hemipenaeus crassipes* Monod 1974:118, figs. 7-11 [= *Aristeus virilis* (Bate 1881) and *Aristeus mabahissae* Ramadan 1938; fide Crosnier 1978:85].

Pseudaristeus crassipes. Crosnier 1978:83, fig. 30*d*; 1986:862.

Pseudaristeus sp. Crosnier 1984:22.

[2]Mayo Deb, Zoologist, Zoological Survey of India, Calcutta, India, pers. commun. 24 November 1984.

Material.

Gulf of Aden—3 ♀, BMNH + 1 ♀, USNM, off Djibouti; 13°06′12″N-13°03′00″N, 46°24′30″E-46°21′42″E; 1,061 m; 7 May 1934; green mud; John Murray Exped. stn 193. 1 ♀, ZMB, off Yemen (Aden); 13°02′N, 46°41′W; 1,469 m; 4 April 1899; *Valdivia* stn 271. 1 ♀, BMNH, off Yemen (Aden); 13°41′N-13°40′N, 48°17′E-48°19′E; 1,295 m; 15 October 1933; John Murray Exped. stn 33. 1 ♀, BMNH, off Yemen (Aden); 14°36′06″N-14°38′42″N, 51°00′18″E-50°57′42″E; 1,269 m; 4 May 1934, John Murray Exped. stn 184.

India—1 ♀, ZMB, Arabian Sea, *Investigator* [stn not given]. 2 ♂, ZSI, S of Cape Comorin, Tamil Nādu; 7°36′N, 78°15′E, 1,017-1,088 m; green mud, sand; 10 April 1900; *Investigator* stn 268. 1 ♀, MP, Gulf of Mannar; 8°11′N, 79°03′E; 1,035 m; 28 July 1981; *Safari II* stn 4, CP 06. 1 ♂, ZSI, off Chidambaran, Tamil Nādu; 11°29′45″N, 80°02′30″E; 816 m; 19 March 1901; *Investigator* stn 280. 1 ♂ 1 ♀, BMNH, S of Andaman Is, 10°06′N, 92°29′E; 1,289 m; *Investigator* stn 315.

Sri Lanka—2 ♀, ZSI, NW of Colombo; 6°54′30″N, 79°34′30″E; 878 m; green mud; 20 October 1898, *Investigator* stn 250.

Indonesia—1 ♀, MP, Strait of Makassar; 2°04′24″S, 118°46′54″E; 1,710-1,730 m; 9 November 1980; *Corindon II* stn 286.

Diagnosis.—Optic calathus relatively short, mesial margin 0.9-1.1 times distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle not expanded laterally; males with ventral antennular flagellum not sinuous and ultimate article of third maxilliped twisted, markedly dilated proximally, less so distally, and bearing ventrolateral rows of minute spines. Pereopods not covered with minute setae. Petasma with distal two-thirds of ventral costa turned rather abruptly distomesially and ventral surface of dorsolateral lobule lacking setae. Thelycum with plate of sternite XIV long and produced in short anterolateral hoods; median plate of sternite XIII moderately long (not nearly reaching spine on sternite XII), rather narrow (maximum width 0.45-0.55 length), and not expanded posterolaterally in conspicuous prominences.

Description.—Body slender, densely studded with minute setae. Rostrum in males (complete only in two) relatively short, its length 0.2 and 0.7 CL, and tapering gradually to sharp apex; in females longer,

1.15-1.25 CL, moderately deep and convex basally, styliform and slightly upturned anteriorly, but occasionally with apical extremity curving downward. Rostral plus epigastric teeth 3; rostral teeth, situated variably in males, basally in females. Adrostral carina strong, in males with short rostrum almost reaching apex, in females and in male with long rostrum extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus crossing postrostral carina (rarely only reaching it) at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt, except for sharp, strongly arched ventral extremity; postcervical sulcus reaching, but not crossing, postrostral carina at about 0.7 CL from orbital margin. Postrostral carina, extending 0.8-0.9 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus before turning obliquely almost ventrad, forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by strong carina, deep and long, extending posteriorly to near margin of carapace; blunt, dorsally concave ridge (disposed dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by shallow groove, latter extending anterodorsally almost to cervical sulcus and continuous posteriorly with postcervical sulcus.

Eye (Fig. 4*A*) with optic calathus relatively short, length of mesial margin 0.9-1.1 times distal width; mesial tubercle strong and situated between 0.30 and 0.45 length of mesial margin from cornea.

Antennular peduncle with stylocerite produced in sharply pointed spine falling distinctly short of, to almost reaching, mesial base of distolateral spine; latter slender and sharp. Third article never produced laterally (Fig. 10*C*); dorsal flagellum reach-

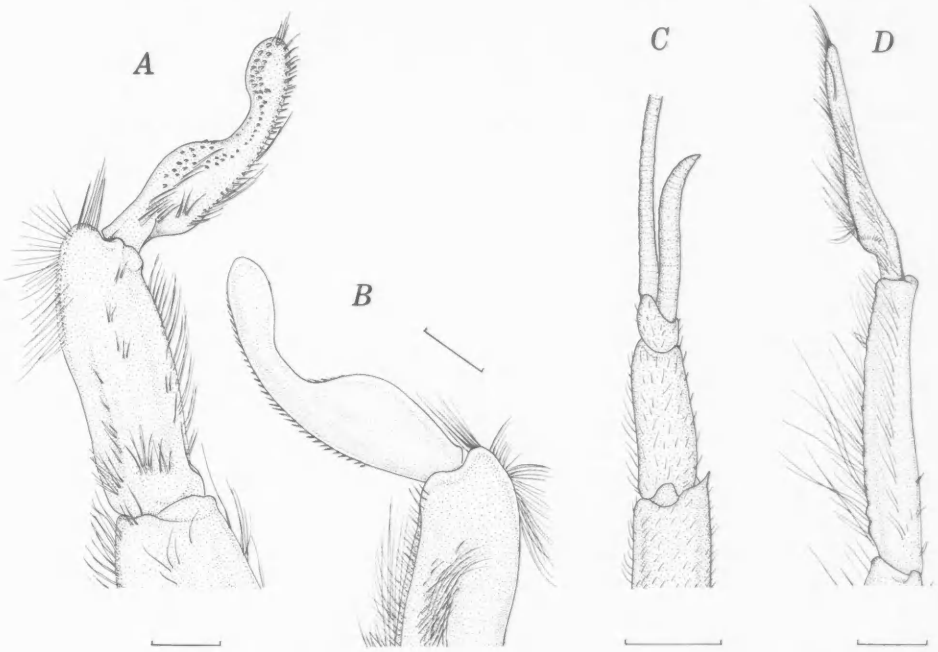


FIGURE 10.—*Pseudaristeus crassipes* (Wood-Mason): *A*, ♂ 26.5 mm CL, south of Cape Comorin, India, distal articles of right third maxilliped, ventral view. *B*, Same ♂ distal articles of right third maxilliped, dorsal view. *C*, Lectotype ♀, Andaman Sea, India, distal articles of right antennular peduncle and flagella, dorsal view (prepared from camera lucida drawings by H. C. Ghosh). *D*, ♀ 25 mm CL, south of Andaman Islands, India, distal articles of left third maxilliped, ventral view. Scales: *A*, *B*, *D* = 1 mm, *C* = 4 mm.

ing between base of distal 0.25 and end of scaphocerite; ventral flagellum straight and long, although broken in all specimens studied, in male with 22 mm CL its length 2.1 times CL.

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum incomplete in all specimens examined.

Third maxilliped sexually dimorphic: Males (Fig. 10*A*, *B*) with penultimate article subtriangular in cross section, its distomesial margin not produced in conspicuous process but bluntly rounded; ultimate article twisted, expanding from short, narrow base, then narrowing and becoming concave laterally before again expanding (sometimes almost imperceptibly) distally; ventral surface with proximal, transverse comb of long setae continuous with lateral rows of minute spines extending to and around distal extremity. Females with ultimate article (Fig. 10*D*), slender, but broadening slightly mesially from short, narrow base, then tapering to blunt apex.

Pereopods not covered with setae; first and second pereopods with broad depressed merus bearing small, slender, distomesial spine.

Abdomen with sharp dorsomedian carina extending along posterior 0.75 of fourth somite through sixth, and produced in spine on posterior margin of last 3 somites; sixth somite also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus shallow, usually distinct only along anterior 0.25 length of telson, and flanked by pair of longitudinal dorsolateral ridges; bearing 4 pairs of movable spines: 3 situated at about 0.60, 0.75, 0.85 length from basal margin of telson, fourth flanking short terminal part. Mesial ramus of uropod surpassing apex of telson by as much as 0.40 its own length; lateral ramus overreaching mesial ramus by as much as 0.33 its length.

Petasma (Fig. 11*A*, *B*) with dorsomedian lobule cincinnulate along entire mesial margin. Ventromedian lobule extending distally almost as far as dorsolateral lobule and bearing elongate, lapel-like flap distoventrally along mesial margin. Dorsolateral lobule sclerotized, not expanded distolaterally, with lateral margin only slightly curved and distalmost part broadly rounded forming subelliptical mesial apex; ventral surface lacking setae, exhibiting conspicuous, slender, arched rib. Ventral costa almost straight basally along 0.4 of its length, then turning somewhat abruptly distomesially, its rather broad terminal part truncate (sometimes with disto-

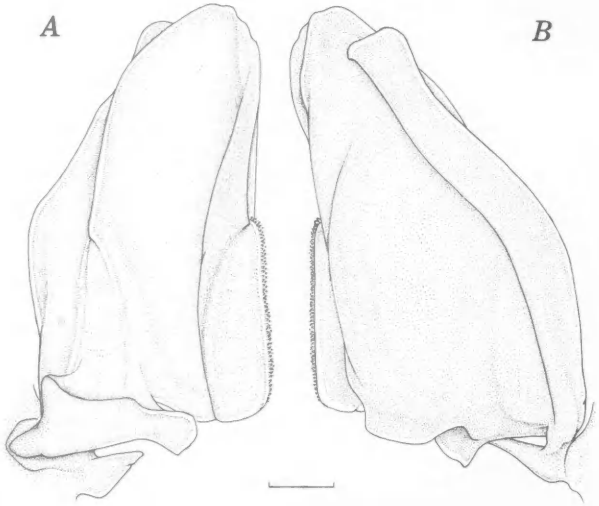


FIGURE 11.—*Pseudaristeus crassipes*, ♂ 26.5 mm CL, south of Cape Comorin, India. *A*, Petasma, dorsal view of left half. *B*, Ventral view (specimen slightly distended). Scale = 1 mm.

mesial angle slightly produced) lying free but against ventral surface of distolateral lobule.

Appendices masculina and interna like those of *P. kathleenae*. In males, plate of sternite XIII flat, ovate but produced in minute apical spine, its length 1.8-1.9 basal width; sternite XIV bearing anteromedian tubercle or low, anteriorly produced prominence.

Thelycum (Fig. 12*A*, *B*) with setose plate of sternite XIV long, transversely depressed (occasionally with median elevation), anteriomedian margin straight or slightly convex, plate produced at either side in short anterolateral hood; fossa immediately anterior to plate short and bearing pair of small, oblique, ridges. Median plate of sternite XIII, also covered with setae, moderately long (length 2.9-3.5 basal width) but falling distinctly short of spine on sternite XII, rather narrow (maximum width 0.45-0.55 length), lanceolate, tapering anteriorly from near base, occasionally from near midlength, and strongly produced in sharp apical spine; posterolateral margins of plate, usually turned ventrally, flanked by, or interlocking with, slender ridges curving laterally on margin of sternite XIII. Sternite XII minutely setose, strongly raised and crested by median carina ending anteriorly in minute spine.

Color in life crimson (Wood-Mason 1891).

Maximum lengths.—Males, 29 mm CL; females 37 mm CL.

Geographic and bathymetric ranges.—From the Gulf of Aden to the Strait of Makassar, Indonesia (Fig. 9). It has been found at depths between 741 and 1,710-1,730 m.

Variation.—This species exhibits marked variation in shape of the last 2 articles of the third maxilliped in armature of sternite XIV of males, and also in the shape of the thelycal plate of sternite XIII in females. Those articles range from moderate to very narrow widths and both the proximal and distal parts of the ultimate article may be imperceptibly to conspicuously dilated. Sternite XIV may bear either an anteromedian tubercle or a low, anteriorly produced prominence. In the few males examined, the presence of a very slender ultimate article of the third maxilliped seems to be correlated with the presence of a prominence, instead of a tubercle, on sternite XIV. Furthermore, in females the thelycal plate of sternite XIII, although always lanceolate, may be broadest near the base, (in most specimens), or as far anteriorly as midlength.

The female from the Strait of Makassar, Indonesia, cited in "Material", was made available to me

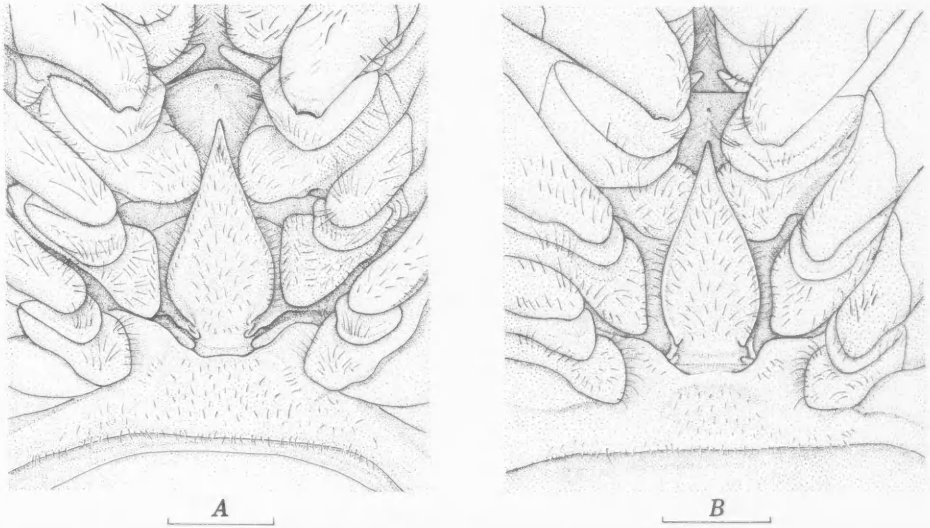


FIGURE 12.—*Pseudaristeus crassipes*: *A*, ♀ 35 mm CL, off Djibouti, Gulf of Aden. *B*, ♀ 35 mm CL, Gulf of Mannar, India. Thelyca. Scale = 2 mm.

through the kindness of A. Crosnier, who discussed this shrimp in his work of 1984. He pointed out features that he believed would distinguish it from *P. crassipes* and *P. sibogae*: the absence of setae from the integument; a narrower median plate on sternite XIII (Fig. 13); the absence of setae on the pereopods [typically present in *P. sibogae* but lacking in *P. crassipes*]; and a robust optic calathus which resembles that of *P. crassipes*.

The Indonesian specimen definitely does not belong to *P. sibogae*, but its relation to *P. crassipes* is not entirely clear. A few specimens of the latter species are glabrous, a condition, as noted by Crosnier, unlikely to have been attained accidentally, but absence of setae is not typical of any species of the genus. Variations in the length/width ratio of the optic calathus of *P. crassipes* embrace that of the Indonesian specimen, the mesial margin length of which is equal to the distal width. The maximum width of the median thelycal plate of sternite XIII in most females of *P. crassipes* ranges from 0.50 to 0.55 its length (in one setose specimen, Figure 12*B*, however, it is only 0.47), whereas the maximum width, 0.45, falls below this range in the Indonesian female. The latter exhibits on the plate of sternite XIV a median ridge that ends in a minute anterior spine, the plate is not produced at either side in an anterolateral hood, and the contour of the median plate on sternite XIII is almost uniformly broad from the base to about midlength. These features differ from those of typical *P. crassipes* females in which the plate of sternite XIV is unornamented, a well-developed anterolateral hood is produced at either side, and the contour of the median plate on sternite XIII broadens from a narrow base posterior to its midlength, then tapers to its apex (cf. Figs. 12, 13). Additional material from the Indonesian locality, including males, might provide evidence for assigning this form to a new taxon.

Discussion.—The males of *P. crassipes* differ strikingly from those of its congeners in that the ultimate article of the third maxilliped is twisted (forming a strong concavity laterally), conspicuously expanded proximally, weakly to markedly dilated distally, and studded with minute spines ventrolaterally. The petasma differs from that of *P. kathleenae* and *P. gracilis*, the other 2 species for which adult males are known; the dorsolateral lobule is not expanded distolaterally, as it is in the former, and it tapers gently to a broadly obtuse apex instead of narrowing rapidly as it does in *P. gracilis*. Furthermore, the ventral costa turns somewhat abruptly distomesiad rather than forming a gentle, sinuous curve or simple arc, and, in contrast to the costa of *P. gracilis*, its terminal part, which is also truncate as it is sometimes in the latter species, is not set off by a conspicuous constriction.

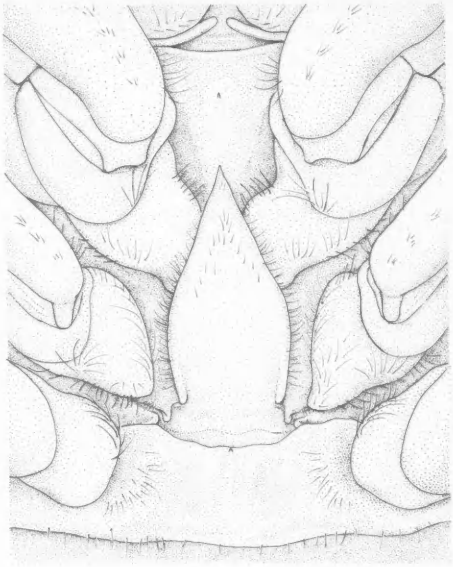


FIGURE 13.—*Pseudaristeus crassipes*, ♀ 35 mm CL, Strait of Makassar, Indonesia. Thelycum. Scale = 2 mm.

The females of *P. crassipes* can be distinguished readily from those of *P. kathleenae* by the shape of the third article of the antennular peduncle, which in the former is uniform in width proximally and tapers distomesially, but in the latter is expanded laterally in a broadly rounded prominence. Also, although the thelyca of these 2 species exhibit a marked resemblance, the median plate of sternite XIII is narrower in *P. crassipes* than that in *P. kathleenae*, its maximum width ranging from 0.45 to 0.55 instead of 0.67 to 0.75.

Remarks.—In the original description of *Aristeus crassipes*, Wood-Mason (1891) cited two females, one from *Investigator* station 116 and another taken at lat. 6°29′N, long. 79°34′E [off southeastern Sri Lanka], perhaps collected by the *Investigator*. He did not designate either specimen as the holotype and consequently they must be considered syntypes. Later, Alcock (1901b) recorded the registration numbers of the various lots of specimens of this

species in the Zoological Survey of India, and next to the number 6713/9, corresponding to the first female cited by Wood-Mason, he added "Types of the species". Immediately following it is the registration number, 3175/9, of the second female (Maya Deb fn. 2). Alcock's referral to "Types" indicate that he did not intend to select the first female as a lectotype; moreover, since he did not specifically designate it as such, according to the Article 74a of the International Code of Zoological Nomenclature of 1961 it cannot be so considered. Maya Deb has also informed me that the female from *Investigator* station 116 is in the Zoological Survey of India accompanied by the registration number cited above, but that the other female recorded by Wood-Mason could not be located. Because two other species, *P. kathleenae* and *P. protensus*, have been confused with *A. crassipes* and conceivably because the missing syntype might prove to be conspecific with one of them, I hereby designate the female in the Zoological Survey of India assigned registration number 6713/9 as the lectotype of *Aristaeus crassipes* Wood-Mason, 1891.

Through the kindness of Maya Deb and H. C. Ghosh, both of the ZSI, who examined the lectotype and provided me with information on specific morphological features, clear drawings, and photographs, I have been able to ascertain the identity of *P. crassipes*. As stated above, the characters used by Wood-Mason in the description of *P. crassipes* were inadequate for distinguishing it from 2 other species and this deficiency was no doubt responsible for the assignments of closely allied forms to *P. crassipes* (De Man 1911, 1913; Kemp and Sewell 1912; Balss 1925). Kemp and Sewell, however, noted that among males of *P. crassipes* in the ZSI there were two types of third maxillipeds which they described and illustrated. They stated further that it was possible that the males exhibiting one of the maxilliped types should be recognized as belonging to a new variety. The "new variety" is described herein as *P. kathleenae*.

Pseudaristeus protensus, new species

Figures 4*D*, 9, 14

Material.

Holotype: ♀, USNM 42681, 40 mm CL, length of median plate of sternite XIII 7.1 mm, basal width 1.5 mm; type-locality W of Evēral Gujārat, India (Arabian Sea); 19°51′30″N, 69°07′30″E; 1,569 m; sand and mud; 14 April 1906; *Investigator* stn 370.

Paratype: ♀, MP, off Godavar, India; 869 m; *Investigator*.

Diagnosis.—Optic calathus relatively short, mesial margin length equal distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle in females not expanded laterally. Pereopods not covered with minute setae. Petasma unknown. Thelycum with plate of sternite XIV very short and produced in long anterolateral hoods; median plate of sternite XIII very long (almost reaching spine on sternite XII), narrow (maximum width 0.40 length), and not expanded posterolaterally in conspicuous prominences.

Description.—Body of holotype and paratype (only two specimens available) slender, studded with minute setiferous punctations and extremely minute setae. Rostrum broken. Anntenal spine broken; branchiostegal spine long, slender, and acutely pointed. Cervical sulcus crossing or just reaching postrostral carina at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt except for sharp, strongly arched ventral extremity; postcervical sulcus deep, almost reaching, but not crossing, postrostral carina at about 0.70 CL from orbital margin, and considerably extending anteriorly. Postrostral carina, extending to 0.85 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus, where turning obliquely almost ventrally forming small branch nearly reaching branchiostegite; branchiocardiac sulcus, accompanied by sharp carina, deep and long, extending posteriorly to near margin of carapace; strong, arched ridge (disposal dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by deep groove, latter continuous posteriorly with postcervical sulcus but not extending anteriorly to cervical sulcus.

Eye (Fig. 4*D*) with optic calathus relatively short, length of mesial margin equal width of distal extremity; mesial tubercle strong and situated at distal 0.33 length of mesial margin.

Antennular peduncle with stylocerite produced in sharply pointed spine almost reaching or falling

short of mesial base of well-developed, sharp, distolateral spine; third article not produced laterally; dorsal flagellum extending to distal 0.2 of scaphocerite; ventral flagellum although incomplete, long, and straight, not mesially curved (concave) just distal to apex of dorsal flagellum.

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length, strong lateral rib ending in acutely pointed small spine falling considerably short of distal end of lamella. Antennal flagellum broken.

Third maxilliped with ultimate article slender but slightly broadening mesially from narrow base, then tapering gently to blunt apex.

Pereopods not covered with setae; first and second pereopods with broad, depressed merus armed with small, slender, distomesial spine.

Abdomen with sharp dorsomedian carina extending full length of fourth somite through sixth, and produced in spine on posterior margin of last 3 somites; sixth somite also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus shallow anteriorly, indistinct posteriorly, and flanked by paired longitudinal dorsolateral ridges (posterior part of telson lacking in types). Lateral ramus of uropod surpassing mesial ramus by about 0.3 its own length.

Thelycum (Fig. 14) with setose plate of sternite XIV very short, deeply excavate transversely, bearing small anteromedian notch, and produced at either side in elongate anterolateral hood; fossa immediately anterior to plate very short and armed with pair of small, oblique lateral ridges. Median plate of sternite XIII very long (length 4.5-4.9 times basal width), narrowly lanceolate (maximum width 0.4 length), strongly produced in sharp apical spine, almost reaching anteromedian spine on sternite XII and covered by very thickly set setae; posterolateral margins of plate raised in slender ridges merging with similar ones extending posteromesially before curving laterally following margin of sternite XIII. Sternite XII minutely setose, strongly raised and bearing low median carina ending anteriorly in minute spine.

Geographic and bathymetric ranges.—Known only from the type-locality, located in the Arabian Sea, and from off Godavari, in the Bay of Bengal, at depths of 1,569 and 869 m respectively (Fig. 9).

Discussion.—Like *P. crassipes*, *P. kathleenae*, and *P. gracillis* but unlike *P. sibogae*, the anterodorsal extremity of the groove dorsal to the posterior part of the hepatic sulcus does not join the cervical sulcus in *P. protensus*; the optic calathus is relatively short, and the pereopods are not covered by setae. *Pseudaristeus protensus* differs strikingly from all its cogeners in several distinctive thelycal features: the plate of sternite XIV is short, bears a small median notch on the anterior margin, and is produced in long anterolateral hoods; the median plate of sternite XIII is very long (4.5-4.9 times the basal width, rather than 1.8-3.5), almost reaching the anteromedian spine on sternite XII, and narrower (maximum width 0.40 instead of 0.45-0.75) than its length. Moreover, it is very densely setose (more so than in its cogeners) and bears a pair of very conspicuous, vertically directed posterolateral ridges.

Although I have examined only two specimens of *P. protensus*, distinct thelycal differences between this gamba prawn and those of other members of the genus leave no doubt that it represents a new species.

Etymology.—Latin *protensus*, stretched forth, referring to the unusual length of the thelycal plate of sternite XIII.

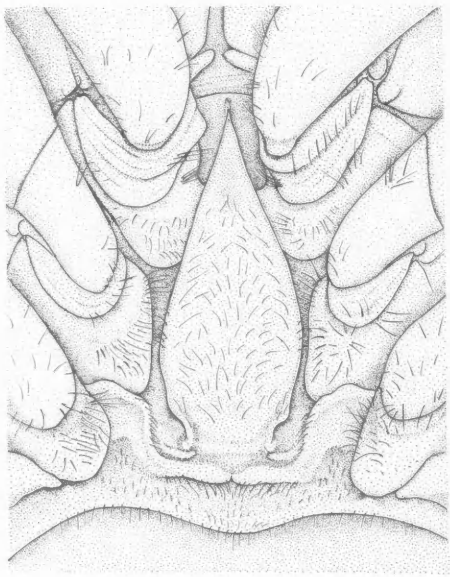


FIGURE 14.—*Pseudaristeus protensus*, n. sp., holotype ♀ 40 mm CL, west of Evēral Gujārat, India. Thelycum. Scale = 2 mm.

Pseudaristeus gracilis (Bate 1888)

Figures 4*B*, 9, 15-17

Hemipenaeus gracilis Bate 1888:302, pl. 44, fig. 2 [syntypes 3 ♂ 3 ♀, BMNH; type-locality: off Tablas I, Philippines; 12°21′N, 122°15′E; 1,240 m; blue mud; 16 January 1975; *Challenger* stn 207]. De Man 1911:26. Estampador 1937:493. Anderson and Lindner 1945:301. Burukovsky 1974:48.

Hemipeneus gracilis. Faxon 1895:198.

Pseudaristeus gracilis. Crosnier 1978:76, fig. 27 bis. 30e.

Material.

Philippines—8 ♀, USNM, Iligan Bay, northern Mindanao; 8°15′20″N, 123°57′E; 750 m; gray mud, sand; 7 August 1909; *Albatross* stn 5511. 1 ♀, USNM, Iligan Bay, northern Mindanao; 8°34′48″N, 124°01′24″E; about 1,280 m; 8 August 1909; *Albatross* stn 5515. 1 ♂, USNM, Macajalar Bay, northern Mindanao; 8°41′30″N, 124°35′40″E; 1,013 m; green mud, fine sand; 4 August 1909; *Albatross* stn 5499. 1 ♂ 2 ♀, USNM, eastern Mindanao Sea; 9°06′30″N, 125°00′20″E; 1,785 m; gray mud; 2 August 1909; *Albatross* stn 5495. 1 ♀, USNM, N of Siquijor I; 9°12′45″N, 123°45′30″E; 1,472 m; green mud, globigerina; 11 August 1909; *Albatross* stn 5526. 1♀, USNM, eastern Mindanao Sea; 9°12′45″N, 125°20′E; 1,344 m; gray mud; 1 August 1909; *Albatross* stn 5492. 1 ♀, USNM, between Bohol and Siquijor Is; 9°22′30″N, 123°42′40″E; 719 m; globigerina ooze; 11 August 1909; *Albatross* stn 5527. 2 ♂ 1 ♀, USNM, eastern Mindanao Sea; 9°24′N, 125°12′E; 1,346 m; green mud, coral; 1 August 1909; *Albatross* stn 5491. 1 ♀, USNM, off Panaon Is, S of Leyte; 9°58′00″N, 125°07′40″E; 1,417 m; green mud; 10 April 1908; *Albatross* stn 5203. 2 ♀, USNM, Sogod Bay, southern Leyte; 10°N, 125°06′45″E; 1,412 m; green mud; 31 July 1909; *Albatross* stn 5488. 1 ♂, USNM, Sogod Bay, southern Leyte; 10°02′45″N, 125°05′33″E; 1,339 m; green mud; 31 July 1909; *Albatross* stn 5487. 1 ♂ 1 ♀, ZSI, Sogod Bay, southern Leyte; 10°10′00″N, 125°04′15″E; 1,013 m; gray sand, mud; 10 April 1908; *Albatross* stn 5201. 2 ♀, MP, SW of Tablas I; 12°09′N, 122°14′E; 1,404 m; 6 June 1985; MUSORSTOM III, stn CP 136. 3 ♂ 3 ♀ syntypes. 1 ♀, MP, SE of Bondoc Point, Luzon; 13°02′08″N, 122°37.1′E; 1,030-1,190 m; 25 November 1980; MUSORSTOM II stn 39. 3 ♂ 3 ♀, MP, NE of Bondoc Point, Luzon; 13°23.2′N, 122°20.7′E; 820-760 m; 26 November 1980; MUSORSTOM II stn 44.

Diagnosis.—Optic calathus relatively short, mesial margin 1.0-1.3 times distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle not expanded laterally; males with ventral antennular flagellum sinuous and ultimate article of third maxilliped straight and slightly broadening proximomesially before tapering to apex. Pereopods not covered with minute setae. Petasma with distalmost part of dorsolateral lobule narrowing to subangular apex, and ventral surface studded with minute setae; ventral costa slightly inclined distomesially and contracted just proximal to spatulate or paddlelike terminal process. Thelycum with plate of sternite XIV short and produced in moderately long anterolateral hoods; median plate of sternite XIII relatively short (not nearly reaching spine on sternite XII), broad (maximum width 0.80-0.93 length), thickened and expanded posterolaterally in conspicuous prominences.

Description.—Body slender, densely studded with minute setae. Rostrum in males short, its length 0.25-0.30 CL and tapering gradually to sharp apex; in females long, 0.90-1.50 CL, relatively deep and convex basally, styliform and slightly upturned anteriorly. Rostral plus epigastric teeth 3; rostral teeth situated variably in males, basally in females. Adrostral carina strong, in males almost reaching apex of rostrum, in females extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus crossing postrostral carina (rarely only reaching it) at about 0.45 CL from orbital margin, ventral part turning anteriorly; accompanying carina blunt, except for sharp, strongly arched ventral extremity; postcervical sulcus reaching, but not crossing, postrostral carina at about 0.7 CL from orbital margin. Postrostral carina, extending to 0.8-0.9 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus before turning obliquely almost ventrad forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by carina, deep and long, extending posteriorly to near margin of carapace; blunt arched ridge, disposed dorsal to posterior part of hepatic sulcus and anterior part

of branchiocardiac sulcus, delimited dorsally by very shallow, sometimes indistinct, groove.

Eye (Fig. 4*B*) with optic calathus relatively short, length of mesial margin 1.0-1.3 times distal width; mesial tubercle strong and variably situated between 0.15 and 0.35 length of mesial margin from base of cornea.

Antennular peduncle with stylocerite produced in sharply pointed slender spine falling distinctly short of, or almost reaching, mesial base of distolateral spine; latter acutely pointed. Third article never produced laterally (Fig. 15*A*); dorsal flagellum about 0.4 length of antennular peduncle, reaching between distal 0.2 and terminal margin of scaphocerite; ventral flagellum long (although incomplete in all specimens examined, in one male 20 mm CL it length 3 times CL), uniquely sinuous, slightly broadened just distal to apex of dorsal flagellum and bearing narrow band of densely set small setae on mesial margin of broadened part (Fig. 15*A*).

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum incomplete in all specimens examined.

Third maxilliped in males (Fig. 15*B*) with penultimate article subtriangular in cross section, and not produced in distal process; ultimate article slender, slightly broadening mesially from short, narrow base before tapering to apex (sometimes slightly dilated proximal to tip); in females (Fig. 15*C*) penultimate article more slender than in males, ultimate article broadening slightly from narrow base then tapering to blunt apex.

Pereopods not covered with setae; first and second pereopods with broad, compressed merus bearing small, slender, distomesial spine.

Abdomen with dorsomedian carina extending from fourth through sixth somite, carina low on fourth, sharp and somewhat higher posteriorly, and produced in small spine on caudal margin of each somite; sixth also bearing pair of minute postero-

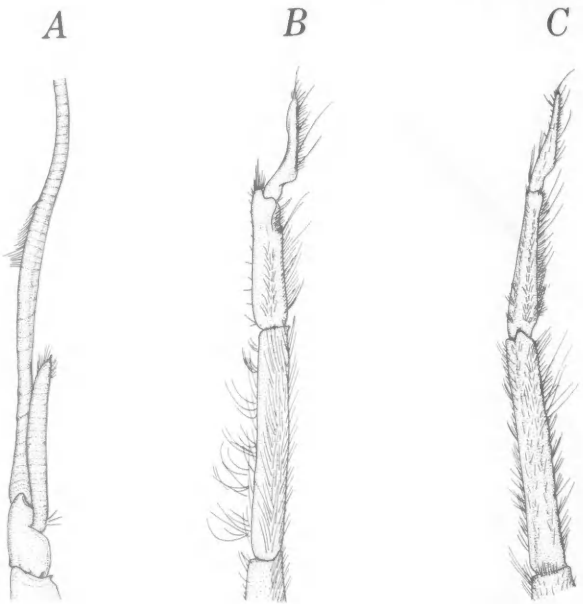


FIGURE 15.—*Pseudaristeus gracilis* (Bate): *A*, ♂ 20 mm CL, eastern Mindanao Sea, Philippines, last article of right antennular peduncle and flagella, dorsal view. *B*, same ♂, distal articles of left third maxilliped, dorsolateral view. *C*, ♀ 35.5 mm CL, between Bohol and Siquijor Islands, Philippines, distal articles of left third maxilliped, dorsal view. Scale = 2 mm.

lateral spines and 2 elongate cicatrices. Telson with median sulcus well defined only on anterior 0.33 length of telson and flanked by paired longitudinal, slender ridges reaching base of third of 4 pairs of movable, marginal spines: 3 situated at about 0.65, 0.80, and 0.90 length from basal margin of telson, fourth flanking short terminal part. Mesial ramus of uropod surpassing apex of telson by about 0.40 its own length; lateral ramus overreaching mesial ramus by about 0.33 its own length.

Petasma in adults (Fig. 16*A*, *B*) with dorsomedian lobule cincinnulate along entire mesial margin. Ventromedian lobule, extending distally as far as dorsolateral lobule, and bearing elongate, lapel-like flap distoventrally along mesial margin. Dorsolateral lobule sclerotized, broad proximally to about base of distal 0.25, then tapering to subacute mesial apex, ventrally bearing conspicuous longitudinal, arched rib and studded with setae. Ventral costa broadly curved along almost entire length, inclined disto-

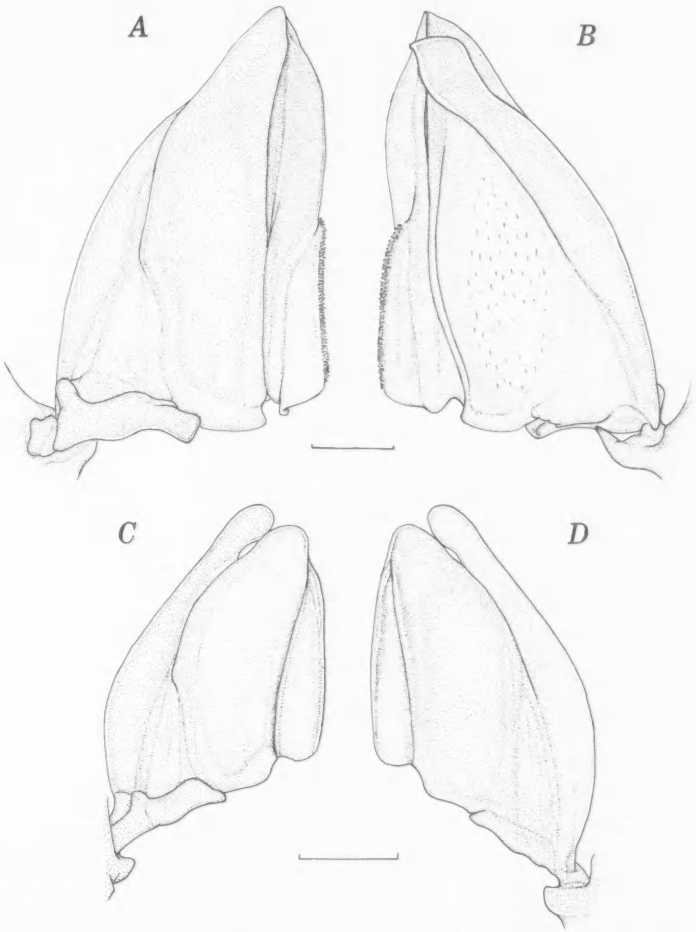


FIGURE 16.—*Pseudaristeus gracilis*, Petasmata: *A*, ♂ 20 mm CL, eastern Mindanao Sea, Philippines, dorsal view of left half. *B*, Ventral view. *C*, Syntype ♂ 13 mm CL, Tablas Island, Philippines, dorsal view of left half. *D*, Ventral view. Scales: *A*, *B* = 1 mm; *C*, *D*, = 0.5 mm.

mesially and with distal part, lying free but against ventral surface of dorsolateral lobule, markedly contracted just proximal to spatulate or paddlelike terminal process.

Petasma in juveniles lacking cincinnuli, specific characters seemingly absent (Fig. 16*C*, *D*): dorsomedian and ventromedian lobules not completely differentiated, but narrow, lapel-like flap present along ventromesial margin; dorsolateral lobule broad proximally, tapering gradually to rounded mesial tip, and with distolateral margin gently curved. Ventral costa arched throughout its length, narrower and contracted distally.

Appendixes masculina and interna as in *P. kathleenae*.

In males, plate of sternite XIV often bearing inconspicuous anteromedian tubercle; plate of sternite XIII flat, roughly lanceolate, produced in sharp spine, its length 1.5-2.3 basal width.

Thelycum (Fig. 17) with densely setose plate of sternite XIV short, deeply grooved transversely, its sharp anteromedian margin turned ventrally, plate produced at either side in moderately long, anterolateral hood; fossa preceding plate long, deep, and bearing pair of small, obliquely disposed ridges. Median plate of sternite XIII, also covered with thickly set setae, concave, and produced apically in acute spine; relatively short (length 2.0-2.7 basal width), falling considerably short of spine on sternite XII, broad (maximum width 0.80-0.93 length), and uniquely expanded in strong posterolateral prominences continuous with slender ridges extending into fossa of sternite XIV. Sternite XII minutely setose, strongly keeled and crested by median carina ending anteriorly in slender, anteroventrally directed spine.

The morphological account above is the first to include adult features. This gamba prawn was named by Bate (1888) on the basis of 6 small juveniles, and the characters pointed out by him have proven inadequate to recognize the species. Subsequent citations to *P. gracilis* have been based only on Bate's information. The material available to me have allowed the detailed descriptions of the petasma, thelycum, and the ventral flagellum of the male which is unique among the members of *Pseudaristeus*.

Maximum lengths.—Males, 21 mm CL; females, 35 mm CL.

Geographic and bathymetric ranges.—Known only from waters of the Philippines (Fig. 9). It has been taken at depths between 719 and 1,785 m.

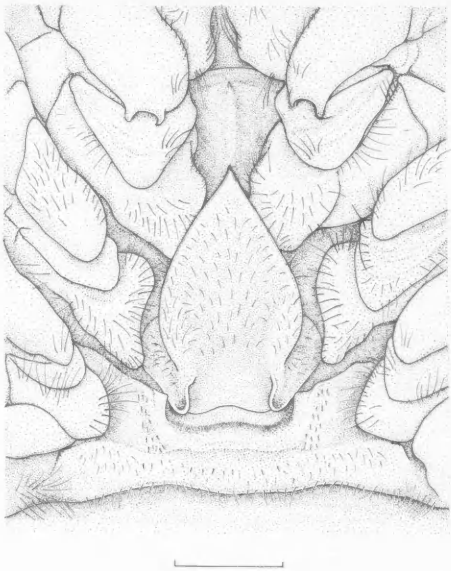


FIGURE 17.—*Pseudaristeus gracilis*, ♀ 35.5 mm CL, between Bohol and Siquijor Islands, Philippines. Thelycum. Scale = 2 mm.

Discussion.—Perhaps the most conspicuous difference between the males of *P. gracilis* and those of the other species of the genus of which males are known is in the ventral antennular flagellum, which is sinuous and bears a dense band of closely set setae on the mesial margin of the slightly broadened part. Males also may be distinguished from those of their cogeners by the shape of the dorsolateral lobule of the petasma, which tapers rapidly to the subangular apex and exhibits a setose ventral surface, and also by the ventral costa, which is markedly contracted distally. Characteristic of the females are the short plate of sternite XIV, in which the anteromedian margin is turned ventrally, and the unique strong posterolateral prominences of the median plate of sternite XIII. The prominences are clearly defined in juveniles as small as the syntype with a 10.3 mm CL.

Pseudaristeus sibogae De Man 1911

Figures 4*E*, 9, 18

Hemipenaeus sibogae De Man 1911:25 [♀ holotype, ZMA De.102.462, E Savu Sea, Indonesia; 9°03′24″S, 119°56′42″E; 1,000 m; globigerina; 20

April 1899; Siboga Exped. stn 52]. De Man 1913, pl. 2, fig. 5, 5a-c. Ramadan 1938:48. Anderson and Lindner 1945:301. Burukovsky 1974:48.

Pseudaristeus sibogae. Crosnier 1978:83, figs. 27a, 30a-c; 1984:22. De Freitas 1985:12, fig. II-5, A-H.

Material.

Madagascar—1 ♀, MP, NW of Ankazomanga; 21°26′30″S, 43°11′00″E; 810-1,020 m; 26 November 1973; *Vauban* stn 92. 1 ♂ 1 ♀, MP, SW of Baie des Assassins; 22°16′48″S, 42°56′00″E; 1,200 m; 30 November 1973; *Vauban* stn 109.

Indonesia—♀ holotype. 1 ♀, USNM, S of Pulau Muna, Sulawesi (Celebes); 5°31′30″S, 122°22′40″E; 834 m; green mud; 16 December 1909; *Albatross* stn 5646. 1 ♂ 2 ♀, USNM, Selat Butung, Sulawesi (Celebes); 5°34′00″S, 122°18′15″E; 950 m; green mud; 16 December 1909; *Albatross* stn 5647. 1 ♀, USNM, off southern Buru; 3°47′15″S, 126°23′40″E; 946 m; fine gray sand; 10 December 1909; *Albatross* stn 5638.

Diagnosis.—Optic calathus long, mesial margin 1.5-1.7 times distal width. Anterolateral carina lacking. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle not expanded laterally; males with ventral antennular flagellum never sinuous; ultimate article of third maxilliped straight and slightly broadening proximomesially before tapering to apex. Pereopods covered with minute setae. Adult petasma unknown. Thelycum with plate of sternite XIV moderately long and produced in short anterolateral hoods; median plate of sternite XIII relatively short (not nearly reaching spine on sternite XII) and broad (maximum width 0.60-0.70 length) but not expanded posterolaterally in conspicuous prominences.

Description.—Body slender, densely studded with minute setae. Rostrum in males straight, moderately long, 0.48 and 0.57 CL in 2 specimens, 21 and 22 mm CL, respectively, and roughly lanceolate; in females longer, in one 37 mm CL its length 1.07 CL, rather deep and usually convex, occasionally almost straight basally, styliform and moderately upturned anteriorly. Rostral plus epigastric teeth 3; 2 rostral teeth in males situated at 0.1-0.2 and 0.4 RL respectively, basally in females. Adrostral carina strong, in both males and females extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus crossing postrostral carina at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt, except for sharp, arched ventral extremity; rather weak postcervical sulcus reaching, but not crossing, postrostral carina at 0.7-0.8 CL from orbital margin. Postrostral carina, extending 0.8-0.9 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastroorbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus before turning obliquely almost ventrad, forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by strong carina, deep and long, extending posteriorly to near margin of carapace; blunt, dorsally concave ridge (disposed dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by groove, latter deep and abutting cervical sulcus anterodorsally but becoming shallow posteriorly and indistinct close to postcervical sulcus.

Eye (Fig. 4*E*) with optic calathus long, length of mesial margin 1.50-1.75 times distal width; mesial tubercle small and situated between distal 0.40 and 0.55 length of margin.

Antennular peduncle with stylocerite produced in sharp, slender spine falling conspicuously short to almost reaching mesial base of distolateral spine; latter acutely pointed; third article never produced laterally. Dorsal flagellum about 0.4 length of antennular peduncle, reaching between distal 0.25 and 0.20 of scaphocerite; ventral flagellum long and straight along entire length.

Scaphocerite extremely long, exceeding antennular peduncle by about 0.30-0.35 its own length; strong lateral rib ending in sharp spine falling considerably short of distal margin of lamella. Antennal flagellum broken in specimens examined.

Third maxilliped in both sexes with penultimate article convex dorsally, slightly flattened ventrally, and not produced in distal process; ultimate article also convex dorsally, slightly excavate ventrally, and slender but broadening slightly from relatively elongate, narrow base before tapering to rather blunt apex.

All pereopods covered with minute setae. First and second pereopods with compressed merus bearing distomesial spine.

Abdomen with dorsomedian carina extending from fourth through sixth somites, carina quite low

but clearly distinct on anterior part of fourth, sharp and rather high more posteriorly, and produced in short but strong spine on caudal margin of each somite; sixth also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus weak, usually limited to anterior half, flanked by paired longitudinal ridges reaching base of second of 4 pairs of movable, marginal spines situated at about 0.55, 0.75, 0.85, and 0.90 length from basal margin. Mesial ramus of uropod surpassing apex of telson by as much as 0.40 its own length; lateral ramus overreaching mesial ramus by as much as 0.33 its own length.

Petasma of young individual lacking cincinnuli, similar to juvenile petasma of *P. gracilis*. Petasma of adults unknown. Curiously, only male available 21.5 mm CL with petasma still quite undeveloped.

Appendices masculina and interna as in *P. kathleenae*.

In small juvenile males, sternite XIV bearing large, minutely setose prominence, semicircular in outline; median plate of sternite XIII setose, elongate (length 2-3 times basal width), and produced in conspicuous apical spine.

Thelycum (Fig. 18) with setose, moderately long plate of sternite XIV broadly depressed and produced at either side in short anterolateral hood, anteromedian margin varying from weakly convex to concave or biconcave; fossa preceding plate relatively short and bearing pair of small, oblique ridges. Median plate of sternite XIII, also covered with setae, relatively short (length 1.8-2.1 times basal width), falling considerably short of anterior margin of sternite XII; broadly lanceolate (maximum width 0.60-0.70 length), produced apically in acute spine, and flat or slightly excavate; posterolateral margins of plate, lacking bosses, abutting slender ridges extending posteromesially before curving laterally on margin of sternite XIII. Sternite XII minutely setose, strongly convex and crested by slender median carina ending anteriorly in sharp spine.

Color, orange (Crosnier 1978).

Maximum lengths.—Males, 22 mm CL (only juveniles known; the 33.5 mm CL cited by Crosnier (1978) is a misprint, the specimen is a female); females, 47.5 mm CL.

Geographic and bathymetric ranges.—This species has been found off Natal, South Africa, western Madagascar, and in the waters of Indonesia to southern Buru (Fig. 9). It occurs at depths between 834 and 1,200 m and was also taken in a trawl between 810 and 1,020 m.

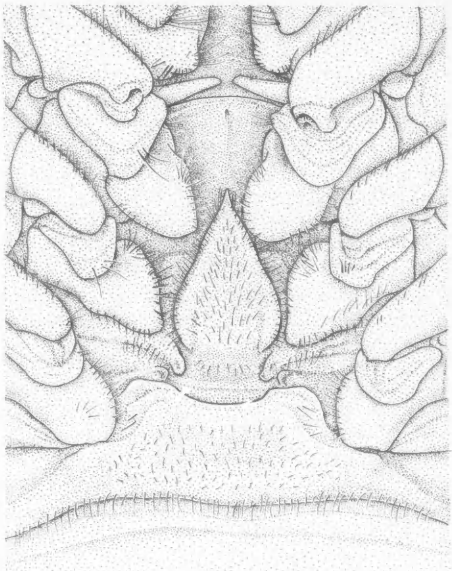


FIGURE 18.—*Pseudaristeus sibogae* (De Man), holotype ♀ 34 mm CL, east Savu Sea, Indonesia. Thelycum. Scale = 2 mm.

Discussion.—The minutely setose pereopods and the disposition of the deep groove lying dorsal to the posterior part of the hepatic sulcus, which abuts the cervical sulcus, distinguish *P. sibogae* from all the species previously described. It also is distinctive in having a longer optic calathus, the length of the mesial margin being at least 1.45 times its distal width instead of not more that 1.30. The tubercle of the calathus in *P. sibogae* is almost always situated near its midlength, between the distal 0.4 and 0.6 length of the mesial margin rather than only as far as 0.4 or more often less, except in the eye of *P. protensus* in which it is placed about at midlength. In females of *P. sibogae* the median plate of sternite XIII is shorter, its length 1.8-2.1 times the basal width, than in females of its congeners, in which the ratio is usually more than 2.1; in occasional specimens of *P. gracilis* it is 2, overlapping the highest ratios observed in *P. sibogae*.

As stated above, the petasma of the adult of this species is not known; however, the very large prominence of sternite XIV, present in the 2 males examined, appears to be a diagnostic feature. These specimens are 21 and 21.5 mm CL and, curiously,

their petasmata are still little developed, lacking cincinnuli and apparently exhibiting no specific character. In other species, males of this size may be identified by petasmal features. It seems worth mentioning that in the 2 males of this species examined by me, the rostrum is slightly longer, 0.48 and 0.47 CL, than it is in most of the males of its congeners in which it ranges between 0.25 and 0.45 CL.

De Man (1911) indicated that the rostral teeth were less prominent in the female holotype of *P. sibogae* than in the female of *P. crassipes* (= *P. kathleenae*) available to him, and that they were situated in a horizontal line, whereas in the latter "a line uniting the tips of the teeth appears distinctly arcuate". Actually, the arrangement of the teeth in females with the same carapace length varies slightly between individuals of the same species, they are usually disposed in an arc, including *P. sibogae*, but sometimes they are arranged in an almost straight line. De Man also noted that in the holotype of *P. sibogae* the rostrum is much shorter [RL/CL = 0.75] and less slender than in the female of "*P. crassipes*". Crosnier (1978), on the basis of the comparison of a female 37 mm CL (RL/CL = 1.07) with the holotype, believed that the difference in the length of the rostrum seemed invalid, that in the holotype the rostrum was in the process of being generated after having been broken.

Pseudaristeus speciosus (Bate 1881)

Figure 19

Hemipenaeus speciosus Bate 1881:186 [syntypes 1 ♂ 1 ♀ (BMNH); type-locality: E of Río de la Plata, Argentina; 36°44′S, 46°16′W; 2,650 fm (4,847 m); 2 March 1876; *Challenger* stn 325]. Bate 1888: 303, pl. 37, Fig. 3, pl. 44, fig. 3. Murray 1896: 388. De Man 1911:26. Estampador 1937:493. Anderson and Lindner 1945:301. Burukovsky 1974:48.

Hemipeneus speciosus. Faxon 1895:198.

Material.—Argentina Basin—♂ syntype (BMNH).

Diagnosis.—Optic calathus relatively long, mesial margin 1.4 times distal width. Anterolateral carina present. Ventral extremity of cervical carina broad and blunt rather than forming sharp-edged arc. Third article of antennular peduncle in females not expanded laterally. Posterior extremity of hepatic sulcus extending posteriorly subparallel to branchiocardiac sulcus, instead of turning ventrally. Petasma and thelycum unknown.

Description.—Based on few notes by Bate (1881), my observations of his illustration and examination of the incomplete cephalothorax of the male syntype. Body slender, lacking setae. Rostrum (Fig. 19) in male relatively short, its estimated length 0.40 CL and roughly lanceolate. Rostral plus epigastric teeth 3; rostral teeth situated at about 0.35 and 0.75 from orbital margin. Adrostral carina strong almost reaching apex. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus reaching but not crossing postrostral carina at about estimated 0.50 CL from orbital margin and well-marked dorsally; accompanying carina weak, its ventral extremity blunt instead of forming sharp-edged arc; postcervical sulcus reaching, but not crossing, postrostral carina at about estimated 0.70 CL from orbital margin. Postrostral carina well marked and sharp to cervical sulcus, low and blunt posteriorly. Anterolateral carina (ventral to gastro-

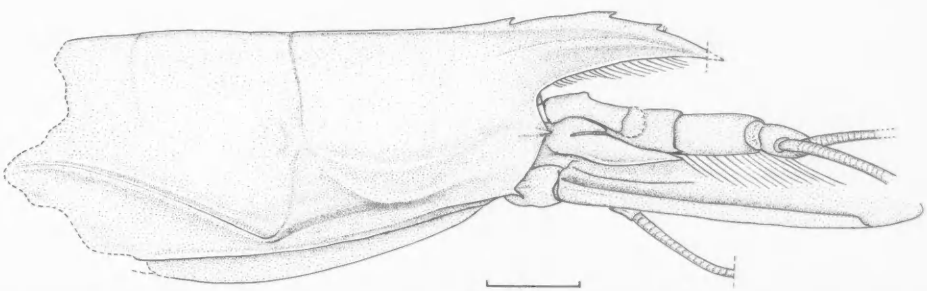


FIGURE 19.—*Pseudaristeus speciosus* (Bate), syntype ♂ "total length = 63 mm" (Bate 1881), off east coast of Buenos Aires. Anterior part of anterior region, lateral view. Scale = 1 mm.

orbital) dorsally concave, rather strong; gastro-orbital carina blunt but well defined; antennal carina relatively short, and branchiostegal-hepatic carina strong and sharp only anteriorly. Orbito-antennal sulcus quite shallow; hepatic sulcus not fusing with branchiocardiac sulcus and extending posteriorly, almost longitudinally rather than turning ventrally, subparallel to anterior part of branchiocardiac sulcus; branchiocardiac sulcus and accompanying carina long, extending posteriorly to near margin of carapace.

Eye with optic calathus relatively long, length of mesial margin 1.4 times distal width; mesial tubercle situated almost at midlength.

Antennular peduncle with stylocerite produced in sharp spine reaching mesial base of distolateral spine; latter small and sharp; third article in females not expanded laterally; dorsal and ventral flagella incomplete.

Scaphocerite long, conspicuously surpassing antennular peduncle; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum incomplete.

Geographic and bathymetric ranges.—*Pseudaristeus speciosus* is known only from the type-locality.

Discussion.—This species, tentatively assigned to the genus *Pseudaristeus*, can be readily distinguished from the other members of the genus in possessing an anterolateral carina; the branchiostegal-hepatic carina is strong and sharp only anteriorly; the ventral extremity of the cervical sulcus is almost straight, instead of turning anteroventrally, and is accompanied by a very weak, rather than sharp, and strongly arched carina; also the posterior part of the hepatic sulcus extends subparallel to the branchiocardiac sulcus instead of fusing with it before turning ventrally.

Pseudaristeus speciosus was described from 2 specimens, one of which is no longer extant and the other has disintegrated except for the anterior part of the carapace to which are attached the eyes, antennules and antennae, and the dismembered distal part of the third maxillipeds. Despite the poor condition of the available syntype, the distinctive features of the carapace, which are clearly represented in Bate's (1888) illustration of the entire animal, are sufficient to conclude that *P. speciosus* is a valid species. Because the branchiae of the syntype are lacking, it is not possible, as noted by Crosnier (1978), to determine with certainty the genus to which it should be assigned, but because of the supraspecific characters exhibited by the carapace, I am almost convinced that it is congeneric with the five Indo-West Pacific species studied herein.

It should be noted that the syntypes of *P. speciosus* were found at 4,847 m, a depth considerably beyond the greatest depth, 1,785 m, at which any of the assumed relatives are known to occur.

ACKNOWLEDGMENTS

Without the generous cooperation of various colleagues this study would not have been possible. I am much indebted to Maya Deb of the Zoological Survey of India for providing descriptions, drawings and photographs of certain morphological features of the lectotype of *P. crassipes*, which permitted a confirmation of the true identity of the species, and for the loan of critical collections from the waters off India; to Alain Crosnier of the Office de la Recherche Scientifique et Technique Outre Mer and the Muséum National d'Histoire Naturelle for his hospitality during a working visit to the latter institution, for the loan of specimens, and for reviewing the manuscript; and to Anthony A. Fincham of the British Museum (Natural History), H.-E. Gruner of the Zoologisches Museum de Humboldt Universitat, and S. Pinkster of the Zoologisch Museum, Amsterdam, for providing materials, including types, from their respective institutions; to H. C. Ghosh of the Zoological Survey of India for a drawing of the antennular peduncle of the lectotype of *P. crassipes*. Horton H. Hobbs, Jr. of the Smithsonian Institution once again offered invaluable advice and innumerable suggestions during the course of my studies and preparation of the paper; Fenner A. Chace, Jr. aided me in solving technical problems and commented on the first draft; Bruce B. Collette and Austin B. Williams of the National Marine Fisheries Service Systematics Laboratory critically read the manuscript. Keiko Hiratsuka Moore, with her artistic talent and devotion to accuracy, made all the illustrations except those of the eyes of various species and the gnathal appendages and of the carapace of *P. kathleenae* which were rendered by María M. Diéguez. Ruth E. Gibbons prepared the map. Virginia R. Thomas and Arleen S. McClain patiently typed several drafts of the manuscript. To all of them goes my deep gratitude.

LITERATURE CITED

ALCOCK, A. W.
1898. A summary of the deep-sea zoological work of the royal Indian Marine Survey Ship "Investigator" from 1884 to

1897. Sci. Mem. Med. Off. Army India 11:45-93.

1901a. Zoological gleanings from the royal Indian Marine Survey Ship *Investigator*. Sci. Mem. Med. Off. Army India 12:35-76.

1901b. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the royal Indian Marine Survey Ship "Investigator". Indian Mus., Calcutta, 286 p.

1902. A naturalist in Indian seas or, four years with the royal Indial Marine Survey Ship "Investigator". John Murray, Lond., 328 p.

ALCOCK, A. W., AND A. R. S. ANDERSON.

1894. Natural history notes from H. M. Indian Marine Survey Steamer "Investigator", Commander, C. F. Oldham, R.N., commanding. Series II, No. 14. An account of a recent collection of deep sea Crustacea from the Bay of Bengal and Laccadive Sea. J. Asiat. Soc. Bengal 63(Part II, 3):141-185.

1899. Natural history notes from H. M. Indian Marine Survey Steamer "Investigator," Commander T. H. Heming, R.N., commanding. Series III, No. 2 An account of the deep-sea Crustacea dredged during the surveying-season of 1897-98. Ann. Mag. Nat. Hist., Ser. 7, 3:1-27, 278-292.

ALCOCK, A. W., AND A. F. MCARDLE.

1901. Illustrations of the zoology of the royal Indian Marine Survey Ship "Investigator," under the command of Commander T. H. Heming, R.N., Crustacea. Part IX, plates 49-55. Off. Supt. Gov. Print. India, Calcutta.

ANDERSON, A. R. S.

1896. Natural history notes from the R.I.M. Survey Steamer "Investigator," Commander C. F. Oldham, R.N., commanding. Series II, No. 21. An account of the deep sea Crustacea collected during the season 1894-95. J. Asiat. Soc. Bengal 65(Part II, 1):88-106.

ANDERSON, W. W., AND M. J. LINDNER.

1945. A provisional key to the shrimps of the family Penaeidae with especial reference to American forms. Trans. Am. Fish. Soc. 73:284-319.

BALSS, H.

1925. Macrura der Deutschen Tiefsee-Expedition, 2. Natantia. Teil A. Wiss. Ergeb. Dtsch. Tiefsee Exped. "Valdivia" 20:217-315.

BATE, C. S.

1881. On the Penaeidea. Ann. Mag. Nat. Hist., Ser. 5, 8: 169-196.

1888. Report on the Crustacea Macrura collected by H.M.S. "Challenger" during the years 1873-76. Rep. Sci. Res. Voyage H.M.S. "Challenger" during the years 1873-76 (Zool.) 24, 942 p.

BURUKOVSKY, R. N.

1974. Opredelitel Krevetok, langoustov i omarov [Keys to shrimps and lobsters]. Moskva Pishch. Promyst'., 126 p. A. A. Balkema (ed.), Rotterdam, 1983, Russ. Trans. Ser. 5, 173 p.

BURUKOVSKY, R. N., AND L. L. ROMENSKY.

1972. The rostrum variability in the shrimp *Aristeus varidens* (Decapoda, Penaeidae) [*In* Russ.]. Rybokhoz. Issled. Atl. Okeane, Tr. AtlantNIRO 42, p. 156-160. Translated by U.S.A. Natl. Mar. Fish. Serv. Int. Act., Wash., D.C., TT 72-50101.

CROSNIER, A.

1978. Crustacés décapodes pénéides Aristeidae (Benthesicyminae, Aristeinae, Solenocerinae). Faune de Madagascar 46:1-197.

1984. Penaeoid shrimps (Benthesicymidae, Aristeidae, Solenoceridae, Sicyoniidae) collected in Indonesia during the *Corindon II* and *IV* Expeditions. Mar. Res. Indonesia No. 24, p. 19-47.

1986. Crevettes pénéides d'eau profond récoltées dans l'océan Indien lors des campagnes *Benthedi*, *Safari I* et *II*, *MD 32/Réunion*. Bull. Mus. Nat. Hist. Nat., Paris, 4e Sér. 7, Sect. A [1985] (4):838-877.

DE FREITAS, A. J.

1985. The Penaeoidea of southeast Africa. II. The families Aristeidae and Solenoceridae. S. Afr. Assoc. Mar. Biol. Res., Oceanogr. Res. Inst., Invest. Rep. No. 57, 69 p.

DE MAN, J. G.

1911. Family Penaeidae. The Decapoda of the Siboga Expedition. Part 1. Siboga Exped. Monogr. 39a, 131 p.

1913. Explanation of plates of Penaeidae. The Decapoda of the Siboga Expedition. Supplement to Part 1. Family Penaeidae. Siboga Exped. Monogr. 39a, (Suppl.), 10 pl.

DOFLEIN, F.

1906. Ostasienfahrt. Erlebnisse und Beobachtungen eines Naturforschers in China, Japan und Ceylon, 511 p.

ESTAMPADOR, E. P.

1937. A checklist of Philippine crustacean decapods. Philipp. J. Sci. 62:465-559.

FAXON, W.

1895. The stalk-eyed Crustacea.Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding, XV. Mem. Mus. Comp. Zool., Harv. Coll. 18, p. 1-292.

FREITAS, A. J. DE. See DE FREITAS, A. J.

KEMP, S., AND R. B. SEYMOUR SEWELL.

1912. Notes on Decapoda in the Indian Museum. III. The species obtained by R.I.M.S.S. "Investigator" during the survey season 1910-11. Rec. Indian Mus. 7:15-32.

LLOYD, R. E.

1907. Contributions to the fauna of the Arabian Sea, with descriptions of new fishes and Crustacea. Rec. Indian Mus. 1:1-12.

MAN, J. G. DE. See DE MAN, J. G.

MONOD, TH.

1974. Sur quelques crustaces neo-caledoniens de profondeur. Cah. ORSTOM, Ser. Oceanogr. 11:117-131.

MURRAY, J.

1896. On the deep and shallow-water marine fauna of the Kerguelen region of the Great Southern Ocean. Trans. R. Soc. Edinb. 38:343-500.

PÉREZ FARFANTE, I.

1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.

1977. American solenocerid shrimps of the genera *Hymenopenaeus*, *Haliporoides*, *Pleoticus*, *Hadropenaeus* new genus, and *Mesopenaeus* new genus. Fish. Bull., U.S. 75:261-346.

1985. The rock shrimp genus *Sicyonia* (Crustacea: Decapoda: Penaeoidea) in the eastern Pacific. Fish. Bull., U.S. 83:1-79.

RAMADAN, M. M.

1938. Crustacea: Penaeidae. Sci. Rep. John Murray Exped. 1933-34, 5(3):35-76.

1952. Contribution to our knowledge of the structure of the compound eyes of Decapoda Crustacea. Lunds Univ. Arsskr. New Ser. Sect. 2, 48(3):1-20.

SEWELL, R. B. S.

1955. A study of the sea coast of southern Arabia. Proc. Linn. Soc. Lond. 165:188-210.

SILAS, E. G., AND M. S. MUTHU.

1979. Notes on a collection of penaeid prawns from the Andamans. J. Mar. Biol. Assoc. India [1976] 18:78-90.

WOOD-MASON, J.
1891. Phylum Appendiculata. Branch Arthropoda. Class Crustacea. *In* J. Wood-Mason and A. Alcock (editors), Natural history notes from H. M. Indian Marine Survey Steamer "Investigator," Commander R. F. Hoskyn, R.N., commanding. Series II, No. 1. On the results of deep-sea dredging during the season 1890-91, p. 269-286. Ann. Mag. Nat. Hist., Ser. 6, 8.

WOOD-MASON, J., AND A. ALCOCK.
1891. Natural history notes from H.M. Indian Marine Survey Steamer "Investigator," Commander R. F. Hoskyn, R.N., commanding. No. 21. Note on the results of the last season's deep-sea dredging. Ann. Mag. Nat. Hist., Ser. 6, 7:1-19, 186-202, 258-272.

YOUNG, J. H.
1956. Anatomy of the eyestalk of the white shrimp, *Penaeus setiferus* (Linn. 1758). Tulane Stud. Zool. 3:171-190.
1959. Morphology of the white shrimp *Penaeus setiferus* (Linnaeus 1758). U.S. Fish Wildl. Serv., Fish. Bull. 59: 1-168.

DISTRIBUTION AND YIELD OF THE DEEPWATER SHRIMP *HETEROCARPUS* RESOURCE IN THE MARIANAS

ROBERT B. MOFFITT AND JEFFREY J. POLOVINA[1]

ABSTRACT

A shrimp trapping survey was conducted at 22 islands and banks in the Mariana Archipelago during a 2-year field period. Three species of deepwater shrimp were found in abundance at various depths: *Heterocarpus ensifer* at 366-550 m, *H. laevigatus* at 550-915 m, *H. longirostris* >915 m. *Heterocarpus laevigatus* was the largest and most abundant of the three and has the greatest economic potential. Estimates of the unexploited biomass of this species by bank were calculated from estimates of catchability, relative abundance, and habitat area. An archipelago average of the unexploited trappable biomass was estimated to be 0.8 t/nmi^2. Evaluation of length-frequency distributions produced estimates of asymptotic length (L_∞) of 55 mm carapace length, instantaneous growth constant (K) of 0.3 yr^{-1}, and instantaneous total mortality (Z) of 0.75 yr^{-1}. A recommended yield of 162.0 t/year (0.2 t/nmi^2 per year) for the entire archipelago was calculated using the Beverton and Holt yield-per-recruit equation based on minimum spawning stock considerations. Of this yield, 85% would come from the southern islands (e.g., Guam and Saipan), 13% from the northern islands (e.g., Pagan and Anatahan), and 2% from the western seamounts (e.g., Arakane Reef and Pathfinder Reef).

The Mariana Archipelago in the western Pacific Ocean stretches from Guam in the south at lat. 13°N to Farallon de Pajaros (also called Uracas) in the north at lat. 20°N (Fig. 1). Within the approximately 270,000 nmi^2 area of the 200 mi zone around the archipelago are two political entities—the Territory of Guam and the Commonwealth of the Northern Mariana Islands (CNMI)—and three geological formations—the southern island chain, the northern island chain, and the western seamount chain (Karig 1971). The purpose of this study was to assess the standing stock and sustainable yield of the deepwater pandalid shrimp resources in the Marianas.

Pandalid shrimp catches account for about 9% of the world shrimp landings or about 155,000 t in 1982 (FAO 1984). About 98% of this catch is of a few species of the genus *Pandalus* trawled at depths of 70-240 m in the cold-water areas of the North Atlantic, North Pacific, and Bering Sea. The next largest pandalid fishery is the trawl fishery for *Heterocarpus reedi* conducted at depths of 155-424 m in the waters off Chili and Peru (Holthuis 1980). The landings from this fishery were 3,450 t in 1982 (FAO 1984). In recent years, pandalid shrimp resources with commercial potential have been identified from deepwater trapping surveys conducted at depths of 200-1,200 m in the central and western Pacific (Clarke 1972; Wilder 1977; King 1980, 1981a, 1981b; Moffitt 1983). The primary component of these catches has been species of the genus *Heterocarpus*, including *H. laevigatus*, *H. ensifer*, *H. sibogae*, *H. longirostris*, and *H. gibbosus*. Trawling for these species has produced poor results (Struhsaker and Yoshida 1975) which may be due to the depths involved, the rough bottom surrounding the Pacific islands, or behavioral characteristics of the shrimp. In Hawaii a rapidly expanding commercial trap fishery has been established with 1983 annual landings of about 135 t. Catches of 1,350 t have been projected for the near future by the Western Pacific Regional Fishery Management Council (WPRFMC 1984). This projected yield has not materialized and does not appear to be forthcoming since the larger shrimp trapping vessels have left the fishery for economic reasons. Commercial ventures in Guam and the CNMI have been sporadic and short lived; landings of 0.3 t were reported in 1982, the last year that the resource was fished.[2]

SAMPLING GEAR AND METHODS

Shrimp trapping operations in the Mariana Archi-

[1]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[2]Western Pacific Fishery Information Network data on file at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

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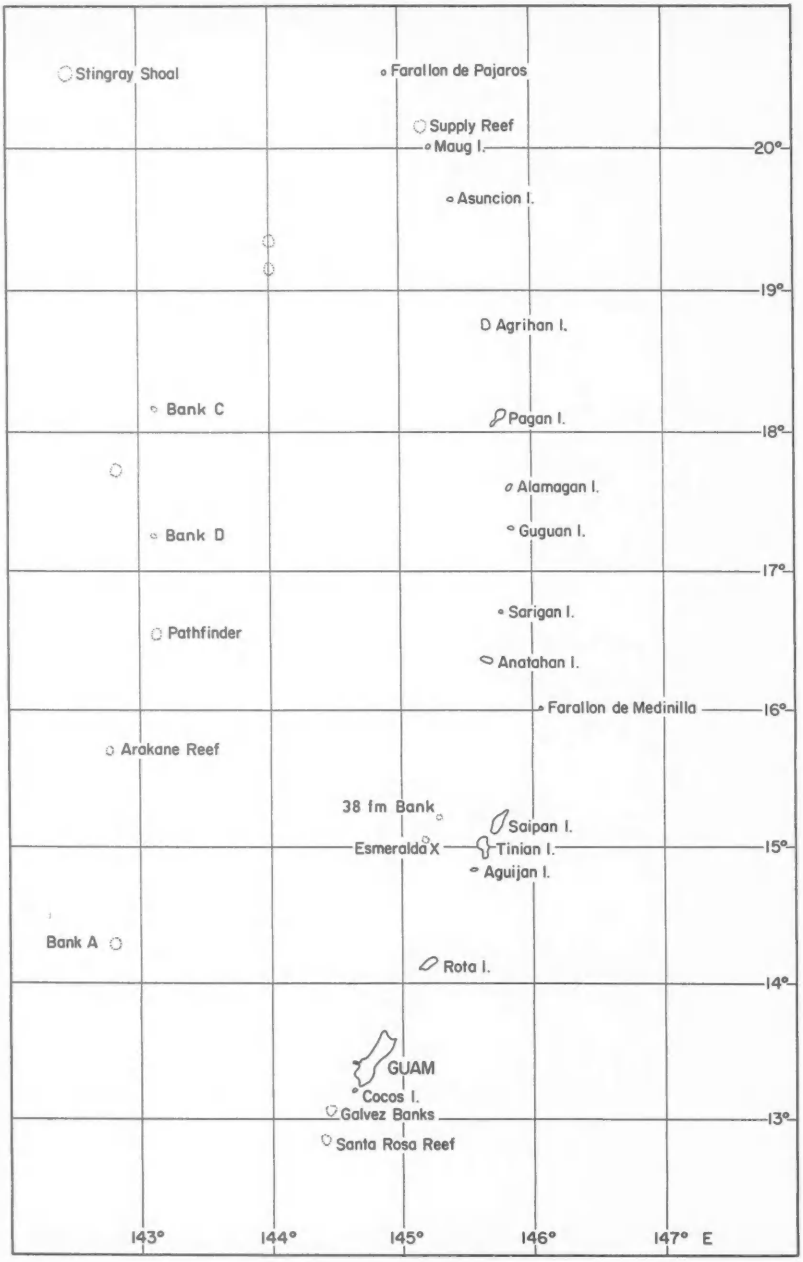

FIGURE 1.—Chart of the Mariana Archipelago.

pelago were conducted on seven cruises of the NOAA ship *Townsend Cromwell* (TC) between April 1982 and August 1984 and one charter cruise of the University of Guam vessel *Pesquedot* (PQ) in August 1984. The standard gear used consisted of strings of five canvas-covered, half-round shrimp traps set about 40 m apart. The traps were constructed of a reinforcing bar frame (about 90 cm long, 65 cm wide, and 45 cm high) wrapped with 2.5 × 1.3 cm mesh, 18-gauge welded wire. An entry cone with an opening of approximately 10 cm was located at each end of the trap. A figure of this general trap design is shown in Gooding (1984). The ground lines attaching the traps together and the main lines attaching the ground line to the surface buoys were of 13 mm polypropylene line. Strings were usually set in the afternoon and retrieved the following morning. Normal soaking times ranged from 15 to 24 hours. Traps were baited with Pacific mackerel, *Scomber japonicus*.

Ordinarily, subsamples of 100 specimens of each of the three major species of *Heterocarpus* (*H. laevigatus*, *H. ensifer*, and *H. longirostris*) were saved each day from each depth sampled. Two sampling sites, Esmeralda Bank and Pagan Island, were visited on each of six *Cromwell* cruises and large subsamples of 400 *H. laevigatus* were saved on each visit. All specimens were returned to the laboratory where the carapace length, sex, and reproductive condition were recorded. The areas of suitable habitat for *H. laevigatus* at each island and bank location was estimated from charts using a computer aided planimeter.

In this study, the yield assessment approach described by Polovina and Ralston (1986) was employed. A systematic survey of 22 islands and banks gave information on the depth range of the primary species and their relative abundance by area. An intensive fishing experiment produced an estimate of catchability using the Leslie method (Ralston 1986). This information combined with an estimate of the area of suitable habitat for each island or bank was used to estimate available biomass by location. Estimates of growth were obtained by application of Elefan I (Pauly 1982) to a site specific time series of length-frequency data. The ratio of mortality to growth and asymptotic length was estimated from a large length-frequency sample (Wetherall et al. in press). Equilibrium yield as a function of fishing mortality was determined from the Beverton and Holt (1956) yield-per-recruit equation as the product of yield per unexploited trappable biomass and the trappable recruited biomass estimate obtained from the systematic sampling and intensive fishing (Polovina and Ralston 1986). Estimates of recommended yield from the equilibrium yield equation were obtained based on marginal yield and minimum spawning stock biomass considerations.

RESULTS[3]

Throughout the course of this survey a total effort of 2,508 trap-nights was expended at 527 shrimp trapping stations. The total catch of pandalid shrimp was 5,188 kg for an overall catch rate of 2.07 kg/trap-night. Over 99% of this catch was composed of *H. ensifer*, *H. laevigatus*, and *H. longirostris*. A complete list of shrimp species taken during this study is given in Table 1.

TABLE 1.—List of shrimp species taken (C = common, F = frequent, R = rare).

Species	Frequency	Depth of abundance (m)
Pandalidae		
Plesionika serratifrons	C	90-270
Plesionika longirostris	C	180-360
Plesionika ensis	F	450-630
Plesionika martia	R	360-450
Heterocarpus ensifer	C	360-540
Heterocarpus gibbosus	R	360-450
Heterocarpus sibogae	R	630
Heterocarpus lepidus	F	540-720
Heterocarpus laevigatus	C	540-810
Heterocarpus dorsalis	F	630-900
Heterocarpus longirostris	C	>900
Heterocarpus tricarinatus	R	900
Oplophoridae		
Acanthephyra eximia	F	810-990
Aristaeidae		
Plesiopenaeus edwardsianus	R	630-810

DEPTH AND SIZE DISTRIBUTION

A plot of catch per unit effort (CPUE) versus depth for the three major species (Fig. 2) shows that they inhabit different depth strata. *Heterocarpus ensifer* is the shallowest dwelling of these species. The maximum catch rate for this species was 0.17 kg/trap-night at a depth of 366 m (200 fathoms). Unfortunately, 366 m was the shallowest depth targeted throughout most of the survey. A small amount of effort was expended in the 137-274 m (75-150 fathoms) depth range on cruises TC-84-02 and PQ-84-01. *Heterocarpus ensifer* catches in this depth range were negligible (only five shrimp in 37 trap-nights). *Heterocarpus laevigatus*, the most abundant shrimp taken in our survey, was caught

[3]Portions of this section are also presented in Polovina et al. 1985.

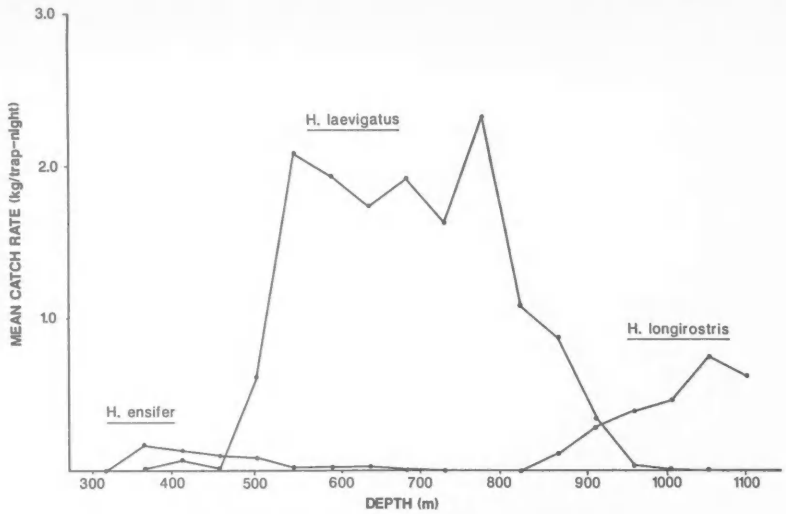

FIGURE 2.—Catch rate of three species of *Heterocarpus* by depth.

in large numbers at depths between 549 and 777 m (300 and 425 fathoms). A maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. *Heterocarpus longirostris* was the deepest dwelling of the *Heterocarpus* species taken, ranging from 823 m (450 fathoms) down past 1,097 m (600 fathoms), which was the greatest depth targeted in this study. Maximum catch rates of *H. longirostris* were obtained at 1,052 m (575 fathoms), but the deeper end of this species' range was not sampled and, as with *H. ensifer*, it is uncertain that the depth of maximum catch rate obtained here is indicative of depth of maximum abundance.

Heterocarpus ensifer was the smallest of the three major species taken. Carapace lengths of 3,401 individuals ranged from 11 to 38 mm with a mean of 26.4 mm. *Heterocarpus laevigatus* was the largest species taken. The mean carapace length was 38.2 mm and the range was 13 to 61 mm (N = 16,405). The mean carapace length of *H. longirostris* was similar to that of *H. laevigatus* ($\bar{x}$ = 37.5 mm), but the size range of 1,443 individuals was more restricted (20 to 50 mm). The mean size of *H. longirostris* taken in this study is probably higher than the mean of catchable shrimp of this species for all depths. We set traps only in the shallower end of this species' depth range (<1,143 m) where the population is dominated by females that grow to a larger size than the males.

It has been suggested that the size of shrimp varies with depth, i.e., larger shrimp occur within the range of maximum abundance while smaller individuals were found in shallower or deeper water (Clarke 1972; Wilder 1977). This type of distribution was not observed for any of the three major species of *Heterocarpus* in the Marianas. Linear regressions of mean carapace length with depth by sex were computed for each of the three species. A significant decrease in carapace length with increasing depth was obtained for *H. longirostris* females, although the full depth range of this species was not sampled. In all other cases, no significant change in size with depth was observed (Table 2).

Wilder (1977) reported high male to female ratios of 3-4 to 1 for *H. ensifer* and *H. laevigatus* taken around Guam. He also stated that small individuals were nearly all males and large individuals almost all female. This was not true for the shrimp examined in this study. The overall sex ratios (ex-

TABLE 2.—Results of mean carapace length by depth regressions for three species of *Heterocarpus* by sex.

Species	Sex	Regression coefficient	R^2	Probability
H. ensifer	Male	0.008	0.41	0.06
	Female	0.002	0.03	0.64
H. laevigatus	Male	−0.007	0.26	0.06
	Female	−0.017	0.16	0.16
H. longirostris	Male	−0.004	0.02	0.83
	Female	−0.04	0.67	0.02

pressed in percent males) for the three major species were 52.8% for *H. ensifer* (N = 3,302), 55.2% for *H. laevigatus* (N = 12,555), and 24.2% for *H. longirostris* (N = 1,408). These ratios tended to hold true for all size classes except the very largest of each species which were indeed nearly all females. Sex ratios did differ by depth showing that the two sexes tend to occupy different areas. In all three major species, females were more abundant at the shallower end of the depth range and males at the deeper end (Fig. 3). This relationship is much more obvious for *H. laevigatus* and *H. longirostris* than for *H. ensifer*. For *H. longirostris*, this may explain the small percentage of males taken in this study since the deeper end of the depth range of this species was not sampled.

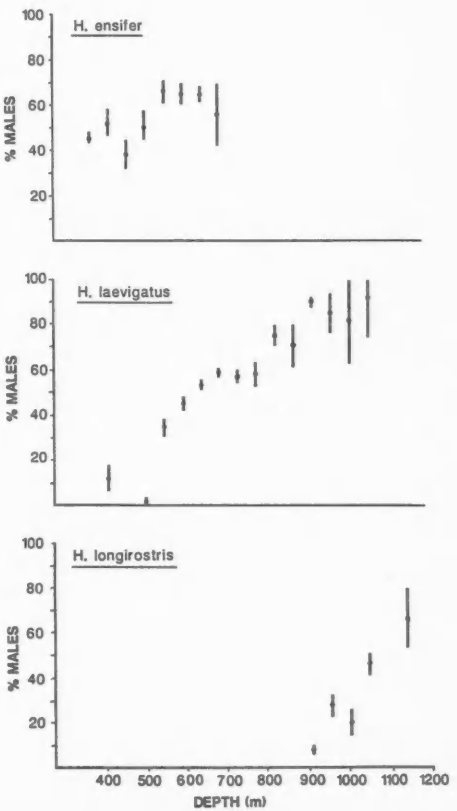

FIGURE 3.—Sex ratio by depth for three species of *Heterocarpus* with 95% confidence limits.

REPRODUCTION

Pandalid shrimp are typically considered to be protandrous hermaphrodites. This is indeed the case for the *Pandalus* species taken in the subarctic areas (Butler 1964). In these species the shrimp spend the first few years of life as functional males, transforming into functional females for the last year or two of life. Clarke (1972) and Wilder (1977) suggested that the tropical *Heterocarpus* shrimp also are protandrous hermaphrodites. The sex ratios obtained in our studies, particularly the near even ratio for the smaller individuals led us to believe that this was not the case. King and Moffitt (1984) examined males of several species of *Heterocarpus* and *Plesionika* for relative growth of the appendix masculina on the second pleopod (a secondary sex characteristic). If these species were indeed protandrous hermaphrodites, the relative size of the male appendage should decrease with increasing carapace length (as the shrimp transforms from male to female). This was not so for any of the tropical pandalids examined. Instead, the relative size of the male appendage increased with increased carapace length indicating maturation as a male. The Marianas data for the ratio (R) of the appendix masculina to the appendix interna versus carapace length (CL) was fit to the logistic model with three parameters, a, b, and c (Gunderson et al. 1980). Table 3 lists the parameters obtained when fitted to the model

$$R \times 100 = \frac{a}{1 + e^{-b(\mathrm{CL}-c)}}.$$

The fit to the nonlinear regression for *H. longirostris* was not particularly good due to the lack of small males in our collection. When the data for this species are fit to a linear regression, however, the slope of the regression is positive indicating relative growth of the secondary sexual characteristics

TABLE 3.—Parameter values for the nonlinear regression of the relative length of the appendix masculina versus carapace length.

Species	a[1]	b	c[2]
Plesionika longirostris	106.83	0.75	11.67
Heterocarpus ensifer	80.35	0.43	15.05
Heterocarpus laevigatus	104.97	0.29	28.09
Heterocarpus longirostris	158.32	0.05	19.36

[1]Asymptotic value for the ratio of the lengths of the appendix masculina and the appendix interna.
[2]Carapace length at the inflection point at 50% of the asymptotic ratio.

with increasing size (regression coefficient = 1.64, r^2 = 0.52).

Based on the assumption that the relative growth of the appendix masculina correlates directly with maturity, we chose the point where this appendage is 90% of its asymptotic value to define the length at maturity for males. The 90% level was used instead of 50% of the asymptotic value, as used for the females below, because the 50% point would be where the males are 50% mature, not where 50% of the males are mature. Using this definition, the carapace length at maturity (L_M) for males of *H. ensifer* is 20.2 mm and that of *H. laevigatus* is 35.7 mm. For *H. longirostris*, the length at maturity is estimated at 31 mm.

The length at maturity of females is perhaps more important in assessment work since the females are directly responsible for the production of recruits to the population. For this study we used the presence of eggs (berried) as the indicator of maturity. The length at maturity is defined as the size where 50% of the females are mature (Gunderson et al. 1980). When using the presence of eggs as the measure of maturity, the sample must be restricted to females collected during the time of year that egg bearing can be expected. For *H. laevigatus*, the breeding season is relatively discrete (November to February), whereas for *H. ensifer* and *H. longirostris* there are peaks in December and May (Fig. 4). Data for each species were fitted to the same nonlinear regression model used for the males. Asymptotic values for percent berried by carapace length are 66% for *H. ensifer*, 92% for *H. laevigatus*, and 55% for *H. longirostris*. The carapace lengths associated with values equal to one-half of the asymptotic values are the L_M for the various species. These are 23.9 mm for *H. ensifer*, 42.7 mm for *H. laevigatus*, and 37.4 mm for *H. longirostris*.

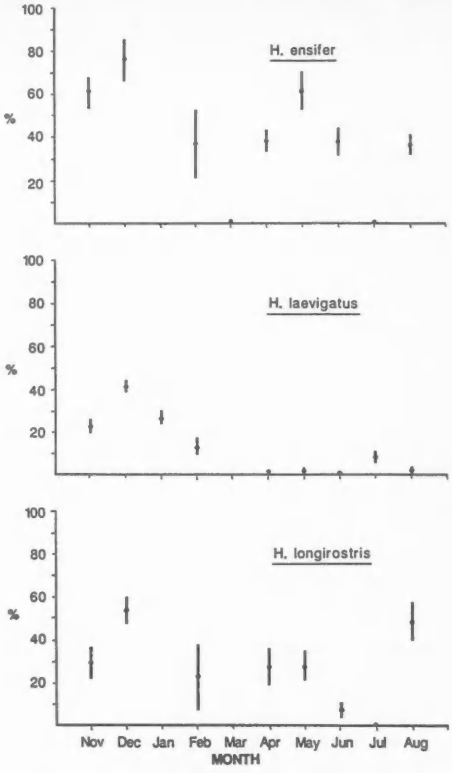

FIGURE 4.—Percentage of females bearing eggs by month for three species of *Heterocarpus* with 95% confidence limits.

YIELD ASSESSMENT

The assumptions and methods of yield assessment used in this study are presented in Polovina and Ralston (1986) and Wetherall et al. (in press). Because *H. laevigatus* yielded the highest catch rates and because it is generally regarded as having superior market acceptability, most of our fishing effort targeted this species. Hence estimates of total biomass and sustainable yield for the pandalid resource are restricted to this species.

GROWTH AND MORTALITY

Estimates of asymptotic size (L_∞) and the ratio of instantaneous total mortality to the instantaneous growth constant (Z/K) were obtained by examining the descending limb of the length-frequency distribution using the regression method based on the Beverton and Holt (1956) model (Wetherall et al. in press). Table 4 lists the values of L_∞ and Z/K for males, females, and pooled sexes for each of the three major species. As anticipated, L_∞ values for females are larger than those for males of the same species. Estimates of length at recruitment to the exploitable population (L_R) were obtained by applying the method of Gulland (1969) to the ascending limb of the same length-frequency distributions. *Heterocarpus ensifer* is recruited into the fishery at a carapace length of 23 mm, *H. laevigatus* at 29 mm, and *H. longirostris* at 34 mm.

By fixing the L_∞ value at the estimates obtained from the large length-frequency sample and using

TABLE 4.—L_∞ and Z/K estimates for the three major species of *Heterocarpus* by sex from length-frequency data.

Species	L_∞	Z/K
Heterocarpus ensifer		
Males	34.5	2.6
Females	37.5	3.0
Sexes combined	36.6	2.9
Heterocarpus laevigatus		
Males	51.3	2.1
Females	55.4	1.9
Sexes combined	55.2	2.5
Heterocarpus longirostris		
Males	41.0	1.7
Females	48.1	1.9
Sexes combined	48.6	2.2

Elefan I (Pauly 1982) to fit the von Bertalanffy growth curve to the time series data for *H. laevigatus* collected at Esmeralda Bank and Pagan Island, the growth constant K can be estimated. When applied to the sexes separately, multiple estimates were obtained for each category ranging from 0.19 to 0.31 yr^{-1}. The inconsistency of these estimates within area and sex groupings was most likely due to the small sample size. When sexes were pooled, however, K was estimated at 0.30 yr^{-1} for both areas. Estimates of the age at recruitment and maturity were obtained by solving the von Bertalanffy equation for the particular carapace lengths estimated above. For female *H. laevigatus*, with a L_R = 29 mm, the T_R = 2.0 years, and with L_M = 43 mm, the T_M = 4.5 years. With a K estimate of 0.3 yr^{-1} and Z/K of 2.5, an estimate for Z of 0.75 yr^{-1} is obtained. Because there is no fishery for *H. laevigatus* in the Marianas, Z is equivalent to natural mortality (M).

UNEXPLOITED BIOMASS

Because standard trapping techniques were used throughout our study, CPUE values from various locations could be used as a measure of relative abundance. The unexploited biomass of the *H. laevigatus* resource for each area is then calculated as the product of the area of suitable habitat and relative abundance divided by the coefficient of catchability (q = 0.001945 trap-night^{-1}) estimated from the Alamagan Island intensive trapping operation (Ralston 1986). Although the catch rate from the western seamounts is about twice that of the southern island chain, the fiftyfold greater area of suitable habitat around the southern islands more than compensates for the low catch rates in producing a higher biomass estimate for the southern islands (Table 5).

TABLE 5.—Catch rates, habitat areas, and unexploited biomass estimates for *Heterocarpus laevigatus* by location.

	Catch rate (kg/trap-night)	Area (nmi^2)	Biomass (t)
Northern Banks			
Maug	1.88	3.83	3.7
Asuncion	2.11	5.93	6.4
Agrihan	1.96	12.39	12.5
Pagan	2.17	16.19	18.0
Alamagan	2.18	11.43	12.8
Guguan	2.52	5.60	7.2
Sarigan	1.45	4.55	3.4
Anatahan	2.36	10.89	13.2
38 Fathom Bank	2.12	6.37	6.9
Esmeralda Bank	1.35	2.03	1.4
Mean =	2.01	Total = 79.21	85.5
Southern Banks			
Farallon de Medinilla	0.97	88.55	44.2
Saipan	2.06	213.99	226.5
Tinian	1.81	73.80	68.4
Aguijan	1.61	39.36	32.6
Rota	1.02	197.31	103.6
Guam	0.48	44.24	16.2
Galvez and Santa Rosa	1.78	50.77	84.5
Mean =	1.39	Total = 708.02	576.0
Seamounts			
Bank C	2.07	2.71	2.9
Bank D	2.72	2.71	3.8
Pathfinder	2.79	2.71	3.9
Arakane	2.83	2.10	2.1
Bank A	1.43	3.33	2.4
Mean =	2.37	Total = 13.56	15.1

EQUILIBRIUM YIELD

With the values for K, L_∞, M, and T_R, the Beverton and Holt yield-per-recruit equation can be used to compute the ratio of equilibrium yield to unexploited recruited biomass (Y/B) as a function of fishing mortality (F) (Polovina and Ralston 1986). Because the shrimp resource in the Marianas is not fished, the estimates of the biomass for each bank represent the unexploited trappable biomass (B), and hence, the product of Y/B and B gives the equilibrium yield as a function of F (Table 6). As F increases, the equilibrium yield increases rapidly for low levels of F. The relationship between F and the equilibrium yield estimated from the Beverton and Holt yield-per-recruit equation assumes that recruitment is unchanged as F increases and does not take into account any economic considerations. Ideally a spawner-recruit relationship is needed to account for changes in yield because of the changes in recruitment which might occur as F increases. However, in the absence of a knowledge of the spawner-recruit curve, two approaches can be used to estimate recommended yield. One approach esti-

TABLE 6.—Equilibrium yield of *Heterocarpus laevigatus* and relative spawning stock biomass as a function of fishing mortality (F).

F	Total yield (t)	Relative spawning stock biomass
0.1	56.2	0.70
0.2	95.6	0.51
0.3	124.2	0.37
0.4	145.4	0.27
0.5	161.6	0.20
0.6	174.1	0.15
0.7	184.1	0.11
0.8	192.0	0.09
0.9	198.5	0.07
1.0	203.8	0.05

mates the recommended yield from the yield-per-recruit derived yield equation as the yield which corresponds to that level of effort where an increase in one unit of effort will increase the catch by 0.1 of the amount caught by the very first unit of effort (Gulland 1983, 1984). This effort is denoted as $F_{0.1}$ and the corresponding yield as $Y_{0.1}$. The value of $F_{0.1}$ for *H. laevigatus* in the Marianas is 0.8 and $Y_{0.1}$ is 192 t annually (Table 6) from areas within the depth range of 500-825 m.

A second approach to estimate recommended yield uses a computation of the spawning stock biomass. With an age estimate of the onset of sexual maturity, the spawning stock biomass for a level of F relative to the spawning stock biomass, in the absence of fishing, can be computed from the Beverton and Holt yield-per-recruit equation (Polovina and Ralston 1986). This relative spawning stock biomass can be used to determine the maximum value of F before a substantial decline in recruitment occurs. The recommended yield can then be estimated as the yield from the constant recruitment yield curve which corresponds to that maximum value of F. This is a conservative approach because it does not incorporate any density dependent compensation, i.e., size at onset of sexual maturity does not decrease as density decreases. The relationship between the relative spawning stock biomass and recruitment is not known for *H. laevigatus*, but it has been suggested that as a lower bound the relative spawning stock biomass should not be reduced below 20% of the unexploited level if a substantial reduction in recruitment is to be avoided (Beddington and Cooke 1983). When F is 0.5, the relative spawning stock biomass is estimated to be 20% of the unexploited level, and the equilibrium yield at this level of fishing is estimated at 162 t annually (Table 6) for the depth range of 500-825 m. To be conservative, the lower yield estimate of 162 t annually from the Mariana Archipelago will be used. Given the habitat area from 500 to 825 m, this yield is equivalent to 0.20 t/nmi^2. An approximate variance for this yield, and hence an approximate confidence interval, can be computed from a Taylor series expansion of the yield estimator if it is assumed that the variance of the yield estimate is due primarily to variances in bank CPUE and catchability. The yield at each bank is computed as

$$\text{Yield} = (\text{CPUE}/q)(\text{Area})(Y/B).$$

Thus the variance of the yield (V(Yield)) can be expressed as

$$V(\text{Yield}) = (\text{Area})^2(Y/B)^2 V(\text{CPUE}/q),$$

$$= (\text{Area})^2(Y/B)^2 \times \left[\frac{V(\text{CPUE})}{q^2} + \frac{(\text{CPUE})^2\, V(q)}{q^4}\right].$$

Estimates of V(CPUE) were obtained from the repeat sampling at each bank and ranged from 0.02 at Guam to 0.64 at Sarigan, while $V(q)$, estimated at 5.5×10^{-7}, was obtained from the intensive trapping work. The variance of the total yield was estimated as the sum of the individual bank variance. The 95% confidence interval, derived from the estimate ± 1.96 times the standard deviation of the estimate of total yield, resulted in a targeted yield range of 102 to 218 t (0.12 to 0.27 t/nmi^2) per year. About 85% of this yield would come from the southern islands and banks, 13% from the northern islands, and about 2% from the western seamounts (Table 7).

DISCUSSION

Although trap design, depth fished, and species present undoubtedly affect catch rate, catch rates reported in other studies using differing trap designs in various areas fall within a fairly tight range of 1.2 to 6.6 kg/trap-night (Table 8). This indicates that the productivity of deepwater pandalids is relatively uniform throughout the tropical central and western Pacific, and the first estimate of recommended yield of 0.2 t/nmi^2 obtained from the Mariana Archipelago can be applied to other Pacific islands, though the relative importance of the various species may differ greatly from area to area.

In our study *H. ensifer*, *H. laevigatus*, and *H.*

TABLE 7.—Equilibrium yield for *Heterocarpus* shrimps in the 500-825 I depth range for a fishing mortality of 0.5.

Bank	Yield (t/yr)
Northern Banks	
Maug	0.9
Asuncion	1.5
Agrihan	3.0
Pagan	4.3
Alamagan	3.0
Guguan	1.7
Sarigan	0.8
Anatahan	3.1
38 Fathom	1.7
Esmeralda	0.3
Total	20.3
Southern Banks	
Farallon de Medinilla	10.6
Saipan	54.1
Tinian	16.3
Aguijan	7.8
Rota	24.7
Guam	3.9
Galvez and Santa Rosa	20.2
Total	137.6
Seamounts	
Bank C	0.7
Bank D	0.9
Pathfinder	0.9
Arakane	0.5
Bank A	0.6
Total	3.6
Archipelago total	161.5

TABLE 8.—Catch rates of pandalid shrimp in the tropical Pacific.

Area	Catch rate (kg/trap-night)	Source
Tonga	1.2	King 1981b
Samoa	1.4	King 1980
Fiji	1.5	King 1983
Hawaii (main islands)	1.5	Clarke 1972
Guam	2.1	Wilder 1977
Mariana Archipelago	2.1	Present study
Hawaii (NWHI)	2.5-3.5	Oishi 1983
Vanuatu	2.8	King 1981a
Hawaii (main islands)	3.5-5.0	Hawaiian Divers, Inc. 1983 (text fn. 4)
Hawaii (main islands)	6.6	Struhsaker and Aasted 1974

longirostris proved to be the major components of the catch within their respective depth zones. *Heterocarpus ensifer* was the shallowest dwelling and the least abundant of the three major species in the Marianas. Its range of abundance was 366 to 503 m (200 to 275 fathoms) and the peak catch rate was 0.17 kg/trap-night at 366 m. In Hawaii, *H. ensifer* appears to be the most abundant species. Average catch rates are between 1.5 and 6.6 kg/trap-night in a somewhat wider reported depth of abundance of 274 to 600 m (Clarke 1972; Struhsaker and Aasted 1974; Gooding 1984). In the Southern Hemisphere; *H. ensifer* is not found in great abundance and is replaced in the 300 to 500 m depth range by a very closely related species, *H. sibogae* (King 1983).

Heterocarpus laevigatus is an important part of the catch throughout the central and western Pacific. In the Marianas, this was the most common species. Its abundance peaked between 549 and 777 m (300 and 425 fathoms) and the maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. In the Northwestern Hawaiian Islands (NWHI), the same standard half-round traps caught just under 1.0 kg/trap-night in an optimum depth range of 500 to 800 m (Gooding 1984). Commercial vessels using larger traps obtained catches of 2.5 to 5.0 kg/trap-night in the Hawaii area and found that the optimum depth range is shallower in the main Hawaiian Islands (530 to 622 m) than in the NWHI (640 to 732 m) (Hawaiian Divers 1983[4]; Oishi 1983; Gooding 1984). In the South Pacific, *H. laevigatus* is reported to be abundant at depths of 549 to 640 m and catch rates range from 0.4 to 1.1 kg/trap-night depending on the area studied (King 1983).

Before this study, *H. longirostris* had been known to science from only four specimens taken in the Indian Ocean (Moffitt 1983). In the Marianas, it occurs in sufficient quantity to suggest a commercial potential. *Heterocarpus longirostris* is probably present in many other areas in the Pacific but has not been found because its optimum depth range is below those sampled.

In the Marianas, sex ratio varied with depth for all three of the major species of *Heterocarpus*. For each species, a larger percentage of the catch is composed of females at the shallower end of the species' depth range. A similar distribution in Hawaii has been reported for *H. ensifer* (Clarke 1972) and *H. laevigatus* (Dailey and Ralston 1986).

Changes in the mean size with depth have been reported for *H. ensifer* and *H. laevigatus*. Wilder (1977) and Gooding (1984) reported increases in size with increasing depth for *H. ensifer* from Guam and the NWHI, respectively. Clarke (1972), on the other hand, found that a higher proportion of larger individuals in Hawaii occupied the depth of greatest abundance, while smaller individuals were found in shallower or deeper water. Gooding (1984) noted a

[4]Hawaiian Divers, Inc. 1983. Deepwater shrimp utilization study for Hawaii. Report prepared under NOAA Cooperative Agreement No. 80-ABH-00065 for the Southwest Region, Western Pacific Program Office, National Marine Fisheries Service, NOAA, 47 p.

decline in size (kilograms/individual) with increasing depth for *H. laevigatus* in the NWHI. In all of these studies, changes in sex ratio with depth were not taken into account. As we have shown, sex ratio does change with depth and the sexes do grow at different rates. The observed changes in size with depth may be due to changes in sex ratio rather than size-specific stratification. Dailey and Ralston (1986) examined the sexes separately and found that for *H. laevigatus* in Hawaii the carapace length of males and egg-bearing females displayed no apparent change with depth, whereas that of nonegg-bearing females showed a strong inverse relationship. In the Marianas, significant changes in mean carapace length with depth were not observed for either sex of the three species of *Heterocarpus*, except for female *H. longirostris* (Table 2). For this group, an inverse relationship was observed much like that found for nonegg-bearing female *H. laevigatus* in Hawaii (Dailey and Ralston 1986).

The estimates of growth parameters for *H. laevigatus* obtained in this study correspond well with those of other authors (Table 9). Using the regression method (Wetherall et al. in press), we estimated L_∞ to be 51.3 mm CL for males, 55.4 mm CL for females, and 55.2 mm CL for the pooled population in the Marianas. Using the same method, Dailey and Ralston (1986) obtained estimates of 57.9 mm CL for males, 62.5 mm CL for females, and 61.7 mm CL for the combined sexes in Hawaii. Apparently, *H. laevigatus* grows about 7 mm larger in Hawaii than in the Marianas. King (1983), using the Beverton and Holt method, estimated L_∞ = 57 mm CL for *H. laevigatus* in Fiji.

Estimates of Z/K for *H. laevigatus* in the Marianas were 2.1 for males, 1.9 for females, and 2.5 for the sexes combined. In Hawaii, Z/K estimates of 4.3, 2.9, and 2.6 were obtained for the same categories, respectively (Dailey and Ralston 1986). The Z/K estimates for the combined sexes are nearly identical in the two studies. In our study, Z/K estimates for the two sexes were similar to each other and lower than that of the sexes combined, whereas in the Hawaii study they were very different from each other and both larger than that of the combined sexes. In our study, if we assume that instantaneous growth of the two sexes is similar, then mortality will also be similar and close to the 0.75 yr^{-1} value estimated for the pooled sexes. In the Hawaii study, Z/K estimates for males and females differed widely. Mortality estimates differed considerably as well, Z = 1.51 yr^{-1} for males and 0.73 yr^{-1} for females.

The K parameter for *H. laevigatus* in the Marianas was estimated as K = 0.30 yr^{-1} for the combined sexes (Table 9). Estimates of K for the individual sexes were ambiguous and inconsistent. King (1983) estimated K as 0.27 yr^{-1} for *H. laevigatus* in Fiji and Dailey and Ralston (1986) estimated K as 0.35 yr^{-1} for male and 0.25 yr^{-1} for female *H. laevigatus* in Hawaii. Because growth estimates for *H. laevigatus* are similar for the various areas studied, it is not surprising that estimates of age at maturity are also similar (Table 9). King (1983) reported the age at maturity for female *H. laevigatus* in the South Pacific as 4.6 years (40.5 mm CL). He further suggests that males mature at about 24 mm CL (age not calculated). Dailey and Ralston (1986) found that females in Hawaii mature at 40 mm or about 4 years. In the Marianas female maturity is estimated at 43 mm CL or about 4.5 years. Males mature earlier at 35.7 mm CL or about 3.0 to 3.5 years. Male maturity estimates by King (1983) and this study are based on the relative growth of the appendix masculina on the second pleopod. King appeared to have chosen 50% of the asymptotic value as the point of maturity much as the point where 50% of the female shrimp are bearing eggs is used to define maturity for females. We feel that 90% of the asymptotic value is a better estimate of male maturity and have used that point in our estimate for the Marianas.

TABLE 9.—Asymptotic length (L_∞), instantaneous growth constant (K), length at maturity (L_M), and age at maturity (T_M) of *Heterocarpus laevigatus*.

Location	L_∞ (mm)	K (yr^{-1})	L_M	T_M
Fiji				
(King 1983)				
Sexes combined	57	0.27		
Females			40.5	4.6
Males			24	
Hawaii				
(Dailey and Ralston 1986)				
Sexes combined	61.7			
Females	62.5	0.25	40	4
Males	57.9	0.35		
Mariana Archipelago				
(present study)				
Sexes combined	55.2	0.30		
Females	55.4		43	4.5
Males	51.3		36	3.5

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LITERATURE CITED

BEDDINGTON, J. R., AND J. G. COOKE.
1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.

BEVERTON, R. J. H., AND S. J. HOLT.
1956. A review of methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch samplings. Rapp. P.-v. Réun. CIEM, 140:67-83.

BUTLER, T. H.
1964. Growth, reproduction and distribution of pandalid shrimps in British Columbia. J. Fish. Res. Board Can. 21: 1403-1452.

CLARKE, T. A.
1972. Exploration for deep benthic fish and crustacean resources in Hawaii. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 29, 18 p.

DAILEY, M. D., AND S. RALSTON.
1986. Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp *Heterocarpus laevigatus* in Hawaii. Fish. Bull., U.S. 84:915-925.

FAO.
1984. 1982 Yearbook of fishery statistics; catches and landings. FAO, Rome 54, 393 p.

GOODING, R. M.
1984. Trapping surveys for the deepwater caridean shrimps, *Heterocarpus laevigatus* and *H. ensifer*, in the Northwestern Hawaiian Islands. Mar. Fish. Rev. 46(2):18-26.

GULLAND, J. A.
1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Fish. Ser. 3, 154 p.
1983. Fish stock assessment. A manual of basic methods. John Wiley & Sons, N.Y., 223 p.
1984. Advice on target fishery rates. Fishbyte [ICLARM] 2(1):8-11.

GUNDERSON, D. R., P. CALLAHAN, AND B. GOINEY.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74-79.

HOLTHUIS, L. B.
1980. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Fish. Synop. (125) vol. 1, 261 p.

KARIG, D. E.
1971. Structural history of the Mariana Islands arc system. Bull. Geol. Soc. Am. 82:323-344.

KING, M. G.
1980. A trapping survey for deepwater shrimp (Decapoda: Natantia) in Western Samoa. Rep. Inst. Mar. Res., Univ. South Pacific, Fiji, 26 p.
1981a. Deepwater shrimp resources in Vanuatu: a preliminary survey off Port Vila. Mar. Fish. Rev. 43(12):10-17.
1981b. The deepwater shrimps of Tonga: a preliminary survey near Nuku'alofa. Rep. Inst. Mar. Res. Univ. South Pacific, Fiji, 29 p.
1983. The ecology of deepwater caridean shrimps (Crustacea: Decapoda: Caridea) near tropical Pacific islands with particular emphasis on the relationship of life history patterns to depth. Ph.D. Thesis, Univ. South Pacific, Suva, Fiji, 258 p.
1984. The species and depth distribution of deepwater caridean shrimps (Decapoda, Caridea) near some southwest Pacific islands. Crustaceana 47(2):174-191.

KING, M. G., AND R. B. MOFFITT.
1984. The sexuality of tropical deepwater shrimps (Decapoda: Pandalidae). J. Crust. Biol. 4(4):567-571.

MOFFITT, R. B.
1983. *Heterocarpus longirostris* MacGilchrist from the Northern Mariana Islands. Fish. Bull., U.S. 81:434-436.

OISHI, F.
1983. Pacific Tuna Development Foundation - State of Hawaii shrimp industry development project. Division of Aquatic Resources, Department of Land and Natural Resources, State of Hawaii, 22 p.

PAULY, D.
1982. Studying single-species dynamics in a tropical multispecies context. *In* D. Pauly and G. I. Murphy (editors), Theory and management of tropical fisheries, p. 33-70. ICLARM and CSIRO, Manila.

POLOVINA, J. J., R. B. MOFFITT, S. RALSTON, P. M. SHIOTA, AND H. A. WILLIAMS.
1985. Fisheries resource assessment of the Mariana Archipelago. 1982-85. Mar. Fish. Rev. 47(4):19-25.

POLOVINA, J. J., AND S. RALSTON.
1986. An approach to yield assessment for unexploited resources with applications to the deep slope fishes of the Marianas. Fish. Bull., U.S. 84:759-770.

RALSTON, S.
1986. An intensive fishing experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Mariana Archipelago. Fish. Bull., U.S. 84:927-934.

STRUHSAKER, P., AND D. C. AASTED.
1974. Deepwater shrimp trapping in the Hawaiian Islands. Mar. Fish. Rev. 36(10):24-30.

STRUHSAKER, P., AND H. O. YOSHIDA.
1975. Exploratory shrimp trawling in the Hawaiian Islands. Mar. Fish. Rev. 37(12):13-21.

WESTERN PACIFIC REGIONAL FISHERY MANAGEMENT COUNCIL.
1984. Status of fisheries assessment of development and management needs for selected crustacean species in the Western Pacific region. Western Pacific Regional Fishery Management Council, Honolulu, HI, 60 p.

WETHERALL, J. A., J. J. POLOVINA, AND S. RALSTON.
In press. Estimating growth and mortality in steady state fish stocks from length-frequency data. *In* D. Pauly and G. R. Morgan (editors), Length-based methods in fishery research. ICLARM Conf. Proc. Manila, vol. 1.

WILDER, M. J.
1977. Biological aspects and fisheries potential of two deepwater shrimps *Heterocarpus ensifer* and *Heterocarpus laevigatus* in waters surrounding Guam. M.S. Thesis, Univ. Guam, Agana, 79 p.

DECLINE IN ABUNDANCE OF THE NORTHERN SEA LION, *EUMETOPIAS JUBATUS*, IN ALASKA, 1956-86

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ABSTRACT

Aerial, ship, and onshore surveys were conducted to assess the abundance of northern sea lions, *Eumetopias jubatus*, in southwestern Alaska, from the central Gulf of Alaska through the central Aleutian Islands, during June-July of 1984-86. Counts of northern sea lions from these surveys were compared with counts made in 1956-62 and 1975-79. These data indicated that the number of adults and juveniles onshore declined 52% from 140,000 animals in 1956-60 to 68,000 in 1985—an annual rate of decline of at least 2.7%. Numbers have declined throughout the region, with the greatest declines in the eastern Aleutian Islands (79%) and the least in the central Aleutian Islands (8%). This was not due to emigration because significant increases have not been noted elsewhere. Between the 1960s and mid-1970s, there were large decreases in the eastern Aleutian Islands and western Gulf of Alaska, and a major increase in the central Aleutian Islands. Beginning in the late 1970s declines occurred in all areas. The causes of the declines are unknown, but they may be associated with disease, prey availability or quality, or a combined effect of these and other factors. Factors which may contribute to the declines include the pre-1973 commercial harvests, entanglement of juveniles in marine debris, incidental takes in fisheries, and killing by fishermen.

The northern or Steller sea lion, *Eumetopias jubatus*, breeds from the Kuril Islands and Okhotsk Sea through the Aleutian Islands and Gulf of Alaska, and south to California. Loughlin et al. (1984) estimated the maximal population in 1974-80 at 290,000 (including some pups), of which more than 196,000 were in Alaska. The number of northern sea lions counted in Alaska was unchanged since the surveys of Kenyon and Rice (1961) and Mathisen and Lopp (1963) in 1956-60, even though significant declines had occurred in the eastern Aleutian and Pribilof Islands (Kenyon 1962; Braham et al. 1980). These declines were offset by increases in northern sea lion numbers in the central and western Aleutian Islands (Fiscus et al. 1981).

Concern over the decline in northern sea lion numbers in the eastern Aleutian Islands prompted the National Marine Mammal Laboratory (NMML) and the Alaska Department of Fish and Game to conduct surveys in 1984, 1985, and 1986 at sites throughout southwestern Alaska. These included aerial, ship, and onshore surveys of rookeries and major haul-out sites from Kiska Island in the central Aleutian Islands to the Barren Islands in the central Gulf of Alaska, as well as observations during two breeding seasons at Ugamak Island, a major rookery in the eastern Aleutian Islands. Together with earlier data for the Aleutian Islands (Kenyon and Rice 1961; Kenyon 1962[3]; Kenyon and King 1965[4]; Braham et al. 1980; Fiscus et al. 1981) and for the Gulf of Alaska (Mathisen and Lopp 1963; Calkins and Pitcher 1982[5]), these data present a 30-yr record of counting northern sea lions, albeit sporadically, in Alaska waters. The objectives of this paper are 1) to report the results of surveys conducted between 1984 and 1986, thus describing the current distribution and numbers of northern sea lions in much of Alaska, 2) to compare those counts with the historical data, and 3) to discuss the state of knowledge on causes of the decline in sea lion numbers.

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FISHERY BULLETIN: VOL. 85, NO. 2, 1987.

[3]Kenyon, K. W. 1962. Sea otter studies, population and distribution (with notes on Steller sea lion and emperor goose). Unpubl. Rep., U.S. Fish Wildl. Serv., Branch Wildl. Res., Seattle, 47 p. Available from Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[4]Kenyon, K. W., and J. G. King, Jr. 1965. Aerial survey of sea otters and other marine mammals, Alaska Peninsula and Aleutian Islands, 19 April to 9 May 1965. Processed Rep., U.S. Fish Wildl. Serv., Bur. Sport Fish. Wildl., Seattle, 52 p. Avaliable from Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115.

[5]Calkins, D. G., and K. W. Pitcher. 1982. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Alaska Dep. Fish and Game, Final Rep. RU243, 128 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

STUDY REGION AND METHODS

Study Region

The study included northern sea lion hauling sites in southwestern Alaska from Kiska Island in the Aleutian Island chain eastward to the Barren Islands in the central Gulf of Alaska (Fig. 1). This region was subdivided for analysis into four areas: 1) central Gulf of Alaska, 2) western Gulf of Alaska, 3) eastern Aleutian Islands, and 4) central Aleutian Islands.

Two general types of northern sea lion sites on land were recognized—rookeries and haul-outs (Loughlin et al. 1984). Rookeries were areas where adult males actively defended territories and most females gave birth and mated. Haul-outs were sites where few pups were present and where little breeding took place. Some islands included more than one distinct rookery and haul-out. A total of 114 sites, of which 28 were rookeries (on 27 islands), were surveyed during 1984-86.

Ugamak Island was a site for NMML field studies during the northern sea lion breeding seasons in 1969, 1977, 1978, 1985, and 1986. The island is located in the eastern Aleutian Islands (long. 164°50′W, lat. 54°14′N), about 110 km east of Dutch Harbor, AK. The island contained the largest aggregation of breeding sea lions in the Aleutian Islands as late as 1969.

Survey Methods

Aerial photographic surveys of northern sea lion rookeries and haul-outs in the eastern Aleutian Islands area (Fig. 1) were conducted 7-12 July 1984, using a Bell 205[6] helicopter flown off of the NOAA ship *Surveyor*. A survey of the entire study region

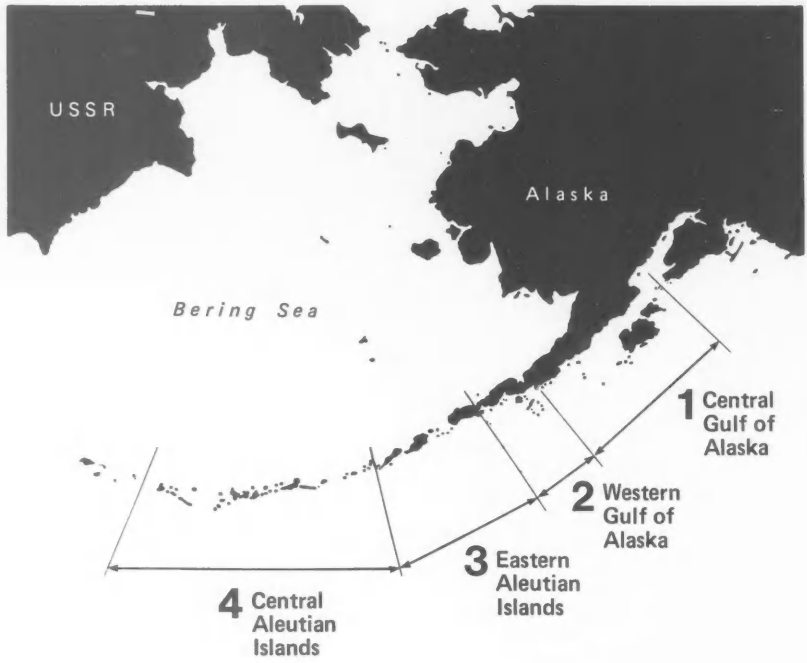


FIGURE 1.—The four Alaskan study areas (left) and 28 northern sea lion rookery sites (right) counted during 1984-86. Rookery island name and number as in Table 2.

was conducted during 9-13 June 1985, using a Grumman Widgeon for the eastern Aleutian Islands and Gulf of Alaska and a Piper Navajo for the central Aleutian Islands. All surveys were conducted between the hours of 1000 and 1800 Alaska Daylight Saving Time (ADT) and from mid-June to mid-July, when the most adult and juvenile sea lions were expected to be onshore (Withrow 1982). Survey methods were those of Braham et al. (1980).

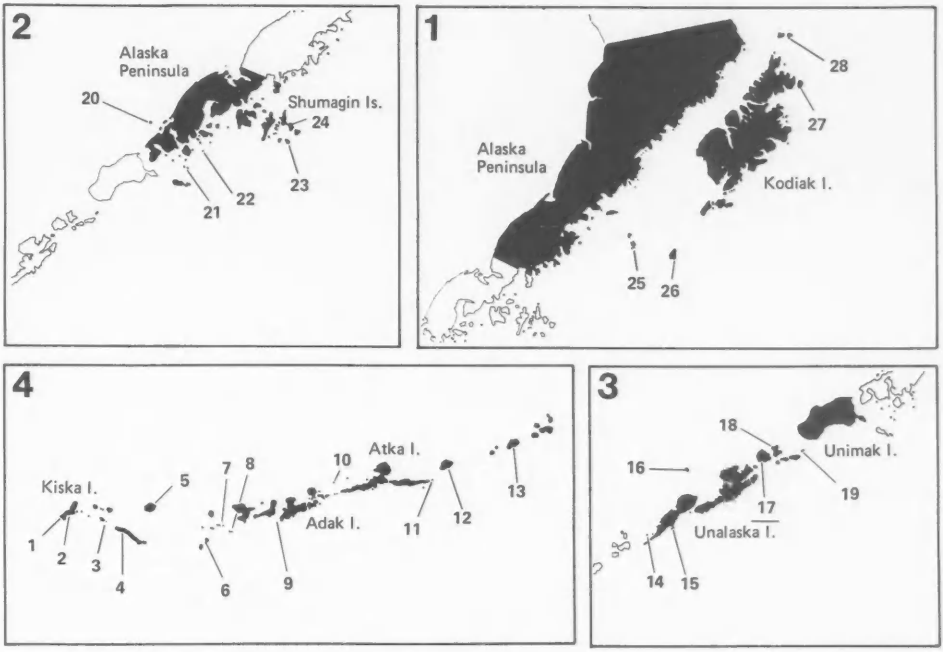
A shipboard survey also was conducted of rookeries and major haul-outs from Ugamak Island to Kiska Island between 25 June and 15 July 1985 (Loughlin et al.[7]). Weather permitting, observers landed at each site and counted the number of northern sea lions present and the number of animals entangled in debris. Pups were counted by first walking through rookeries to drive off the adult and juvenile animals, and then returning to count the pups. This survey was timed to occur after most pups had been born, and before they had begun to enter the water (Withrow 1982).

Pups were counted at northern sea lion rookeries in the central and western Gulf of Alaska between 3 July and 9 July 1984 (Calkins[8]) and between 29 June and 10 July 1986. Access was provided by a skiff launched from a larger vessel or by helicopter.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Loughlin, T. R., P. J. Gearin, R. L. DeLong, and R. L. Merrick. 1986. Assessment of net entanglement on northern sea lions in the Aleutian Islands, 25 June-15 July 1985. Processed Rep. 86-02, 50 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[8]Calkins, D. G. 1985. Draft final report. Steller sea lion pup counts in and adjacent to Shelikof Strait. Submit. to North Pac. Fish. Manage. Coun., March 8, 1985, 13 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.



1, 2 Kiska
3 Ayugadak
4 Amchitka
5 Semisopochnoi
6 Ulak
7 Tag
8 Gramp
9 Adak
10 Kasatochi
11 Agligadak
12 Seguam
13 Yunaska
14 Adugak
15 Ogchul
16 Bogoslof
17 Akutan
18 Akun
19 Ugamak
20 Sea Lion Rock
21 Clubbing Rocks
22 Pinnacle Rock
23 Chernabura
24 Atkins
25 Chowiet
26 Chirikof
27 Marmot
28 Sugarloaf

Pups were counted by driving off the adult animals just ahead of the counting team.

Counts of northern sea lions were made daily by observers on Ugamak Island between 1 June and 3 July 1985 and between 16 June and 26 July 1986. Hourly counts were made between the hours of 0700 and 2400 ADT for 6 days in 1986. Animals were counted from the cliffs above the sites, using 7 × 35 binoculars, a 15-60 power spotting scope, and unassisted vision. Counts were made of animals according to five types: adult territorial male, other adult male, adult female, juvenile, and pup (Merrick 1984). Animals in the water were excluded from counts. Freshly dead pups were recorded when seen, with pup mortality estimated as the total number of dead pups divided by the maximal number of pups counted (living and dead).

Data Analysis

The number of northern sea lions counted in the 1984-86 surveys were compared with counts from surveys in 1956-79 conducted by Kenyon and Rice (1961), Kenyon (fn. 3), Mathisen and Lopp (1963), Braham et al. (1980), Fiscus et al. (1981), and Calkins and Pitcher (fn. 5). Differences in survey areas complicated comparisons for the entire region, so comparisons were generally performed by area.

Comparisons also were complicated by the differences in the counting methods used. Some were counts from land (Fiscus and Johnson 1968[9]; Fiscus et al. 1981; Withrow 1986[10]), while others were estimates from ships (Fiscus and Johnson fn. 9; Calkins and Pitcher fn. 5), and counts from aerial photographs (Mathisen and Lopp 1963; Braham et al. 1980; Calkins and Pitcher fn. 5). The most accurate were visual counts from land and from aerial photos (Withrow 1982); these were the methods used in the 1984-85 aerial surveys.

Several assumptions were made in the analysis of these data. The first was that all sites with more than a few animals were surveyed in 1984-85. Second, the dates and times of peak seasonal and daily abundance were considered to have remained constant throughout the 30-yr period. The 1984-85 surveys and those conducted by Braham et al. (1980) were scheduled to coincide with these peaks; whereas, those of Kenyon and Rice (1961) and Kenyon (fn. 3) were conducted in the spring and without regard to time of day. A smaller proportion of animals were probably onshore in the spring than in the summer (Mathisen and Lopp 1963; Braham et al. 1980). Third, the proportion of the population onshore was assumed to have remained unchanged in the 30 years of counting. Finally, double counting was considered to be negligible in all the surveys because large areas were surveyed in a single day.

Counts presented here are indices of population size because they exclude animals at sea and because it is difficult to count at the exact time peak numbers are ashore. There are few data on the proportion of animals that are at sea at the time the peak number is onshore. Consequently, it was necessary to assume that the proportion had not changed over time. Even during the period when maximal numbers of animals were expected onshore there was variation due to weather and tidal affects (Withrow 1982; Merrick 1984), so that it was unlikely that a survey would occur on the day and time of peak numbers. However, because the sites on Ugamak Island were counted daily, the maximal number counted there was a closer approximation than the aerial survey counts of the actual peak number of animals onshore during the breeding season. Thus the Ugamak Island data were used to determine if seasonal and daily variation in northern sea lion hauling patterns had changed and to assess the potential amount of error (due to counting at the wrong time) in the aerial photo counts.

Rates of decline between two points in time were calculated using the formula

$$N_t = N_0 d^t$$

where N_0 = count in base year
N_t = count in future year t
t = number of years between the base year and year t
d = rate of change, with the percent annual change calculated as $(d - 1) \times 100$.

Area counts were regressed as a linear function of time to determine if trends in population sizes existed. Student's t-test was used to assess the significance of the regressions. Wilcoxon's signed rank test was used for between year comparisons of paired site counts within an area (Hollander and Wolfe 1973).

[9]Fiscus, C. H., and A. M. Johnson. 1968. Site for research on the Steller sea lion, June-July 1968. Processed Rep., U.S. Fish Wildl. Serv., Bur. Commer. Fish., Mar. Mammal Biol. Lab., Seattle, 33 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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RESULTS

1984-86 Survey Findings

The 1984 survey of the eastern Aleutian Islands resulted in a count of 9,833 adult and juvenile northern sea lions on 16 sites (Table 1). The six rookery islands surveyed included 7,934 animals (Table 2), 91% of the total count. One rookery, Adugak Island, and several haul-out sites were not surveyed owing to inclement weather.

A total of 10,802 adult and juvenile northern sea lions were seen in the 1985 survey of the eastern Aleutian Islands (Table 1), which was not significantly different from the 9,833 animals counted there in 1984 ($P > 0.05$). A total of 67,617 animals were counted at 105 sites in the entire study region. Most (60%) of the animals were associated with the 27 rookeries surveyed; the largest rookeries were in the central Gulf of Alaska, notably at Marmot Island, and in the Central Aleutian Islands. The rookery on Semisopochnoi Island was not surveyed; eight previously identified haul-out sites were unoccupied.

Observers in the 1985 shipboard survey counted 4,950 pups at six rookeries in the eastern Aleutian Islands and 9,170 pups at nine rookeries in the central Aleutian Islands (Table 3). In the 1984 and 1986 pup surveys of six rookeries in the Gulf of Alaska (Table 3) 16,278 (excluding Clubbing Rocks and Pinnacle) and 12,025 pups were counted, respectively.

TABLE 1.—Counts and percent declines of adult and juvenile northern sea lions at all sites in spring and summer 1956-85 in the Aleutian Islands and Gulf of Alaska.

	Region				
Year	Central Gulf of Alaska	Western Gulf of Alaska	Eastern Aleutian Islands	Central Aleutian Islands	Reference[1]
1956		[2]24,320			1
1957	35,150				1
1959				28,115	2
1960			[2]52,530		2
1962				31,040	3
1975			21,221		4
1976	30,677	9,480	22,142		4,5
1977			23,922		4
1978		14,917			5
1979				[2]41,677	6
1984			9,833		7
1985	24,389	6,667	10,802	25,759	7
Decline[3]					
Overall	−31%	−73%	−79%	−8%	
Annual	−1.3%	−4.4%	−6.1%	−0.3%	

[1]Reference: 1—Mathisen and Lopp (1963); 2—Kenyon and Rice (1961); 3—Kenyon (text fn. 3); 4—Braham et al. (1980); 5—Calkins and Pitcher (text fn. 5); 6—Fiscus et al. (1981); 7—this study.
[2]Significant difference ($P < 0.05$) from 1985 using Wilcoxon signed rank test.
[3]Declines calculated from earliest survey date.

Trends in Regional Numbers

Comparison of the 1984-85 aerial surveys with historical data (Table 1) shows that significant ($P < 0.05$) declines have occurred in northern sea lion numbers in the western Gulf of Alaska (−73%), and eastern Aleutian Islands (−79%). The central Gulf of Alaska (−31%) and central Aleutian Island populations may have also declined since 1957-59, though the decreases (−31% and −8%, respectively) were not statistically significant ($P > 0.05$). Note that the central Aleutian Islands numbers increased 34% between 1959 and 1979. This suggests that either the population increased markedly, was supplemented by immigration from other areas (e.g., the eastern Aleutian Islands), or was an artifact of the 1979 survey methodology (i.e., a shipboard survey). Linear regression models (Fig. 2) fitted to these counts indicate that the trends of all areas, other than the central Aleutian Islands, exhibit significant negative slopes ($P < 0.05$).

The number of adult breeding animals has declined in all areas since 1957 except the central Aleutian Islands (Table 2). Numbers at the central Aleutian Islands rookeries increased by 88% between 1959 and 1985, a significant increase ($P < 0.01$). As the overall population in the central Aleutian Islands decreased between 1959 and 1985, this may indicate that a larger proportion of the population is now breeding than in the past. Rookery populations in the eastern Aleutian Islands have declined 79% since 1957, a significant decline ($P < 0.05$). A loss of 15,000 animals occurred at the Ugamak and Akutan Island rookeries alone between 1968 and 1975. Numbers at rookeries in the western and central Gulf of Alaska decreased 66% and 47%, respectively, between 1956-57 and 1985.

Trends in Regional Pup Production

Pup counts are available for only a few sites prior to 1984. These data (Table 3) show that the number of northern sea lion pups counted in the central Gulf of Alaska decreased between 1979 and 1986 by 44%, from 18,998 to 10,600. The number of pups has also declined at sites in the western Gulf of Alaska and eastern Aleutian Islands. Pupping decreased 52% at Bogoslof Island between 1968 and 1985, 89% at Walrus Island (in the Pribilof Islands) between 1960

TABLE 2.—Counts of adult and juvenile northern sea lions on individual rookeries for selected surveys from spring and summer 1956 to 1985 in the Aleutian Islands and Gulf of Alaska.

	Year					
Island[1]	1956-59[2]	1960-62[3]	1968[4]	1976-79[5]	1984[6]	1985[6]
Central Aleutians:						
Kiska (1, 2)	1,000	600		7,155		3,066
Ayugadak (3)	600	1,005		1,463		702
Amchitka (4)	600	1,515		1,943		728
Semisopochnoi (5)	2,500	3,700		1,223		nc
Ulak (6)	1,500	550		3,068		2,729
Tag (7)	400	200		1,740		944
Gramp (8)	700	0		2,235		1,290
Adak (9)	0	0		972		964
Kasatochi (10)	200	2,000		2,166		1,170
Agligadak (11)	250	3,000		993		514
Seguam (12)	25	1,275		6,493		2,942
Yunaska (13)	800	110		2,249		1,071
Total	[7]8,575	13,955		[7]31,700		16,120
Eastern Aleutians:						
Adugak (14)	1,275	1,000	nc[8]	1,177	nc	955
Ogchul (15)	2,966	2,000	nc	1,109	712	547
Bogoslof (16)	2,136	1,100	3,310	3,308	1,379	1,287
Akutan (17)	9,275	15,720	10,316	4,019	2,533	1,710
Akun (18)	nc	2,000	1,900	1,050	760	435
Ugamak (19)	14,536	13,400	13,553	4,760	1,252	1,429
Sea Lion Rock (20)	2,871	2,000	nc	2,076	1,298	538
Total	33,059	[7]37,220	29,079	[7]17,499	7,934	6,901
Western Gulf:						
Clubbing Rocks (21)	1,556			2,663		1,251
Pinnacle Rock (22)	3,142			3,692		1,588
Chernabura (23)	4,806			2,758		487
Atkins (24)	4,995			3,943		1,562
Total	14,499			13,056		4,888
Central Gulf:						
Chowiet (25)	6,014			4,441		2,059
Chirikof (26)	1,695			5,199		2,346
Marmot (27)	3,866			6,381		4,983
Sugarloaf (28)	11,963			4,374		2,991
Total	23,538			20,395		12,379

[1]Rookery island name and code (within parentheses) as in Figure 1.
[2]Mathisen and Lopp (1963).
[3]Kenyon (text fn. 3), for central Aleutian Islands in 1962; Kenyon and Rice (1961), for eastern Aleutian Islands in 1960.
[4]Fiscus and Johnson (text fn. 9).
[5]Fiscus et al. (1981), for central Aleutian Islands in 1979; Braham et al. (1980), for eastern Aleutian Islands in 1976; Calkins and Pitcher (text fn. 5), for western Gulf of Alaska in 1978 and central Gulf of Alaska in 1979.
[6]This study.
[7]Significant difference from 1985 at $P < 0.05$.
[8]nc = not counted.

and 1984, and 76% at Akutan Island between 1965 and 1985 (NMML[11]).

Ugamak Island Surveys

The estimated number of sea lions on Ugamak Island was 14,536 in 1957 and 13,553 in 1968 (Table 2). Significant changes were not observed until 1975-78 (Braham et al. 1980), by which time numbers had fallen to about 4,760 animals. Aerial surveys in 1984 and 1985 found 1,252 and 1,429 animals, respectively.

Ground counts of sea lions on Ugamak Island at comparable sites and survey dates (Table 4) showed a decline of 84% from 10,295 in 1969 to 1,684 in 1986. The decline was greatest between 1969 and 1977 when the count fell by 65%, from 10,295 to 3,577. Numbers fell 53% from 1977 to 1986, and 17% between 1985 and 1986.

The number of breeding animals at Ugamak

[11]Data available from NMML files. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

TABLE 3.—Counts of northern sea lion pups at sites in the Aleutian Islands and Gulf of Alaska, 1978-86.

Island	Year 1978[1]	1979[1]	1984[1]	1985[2]	1986[2]
Central Aleutian:					
Kiska				882+	
Ayugadak				329	
Amchitka				nc	
Semisopochnoi				nc	
Ulak				1,236	
Tag				703	
Gramp				909	
Adak				558	
Kasatochi				892	
Agligadak				nc	
Seguam		2,475		2,635	
Yunaska				1,026	
Total		2,475		9,170+	
Eastern Aleutian:					
Adugak				844	
Ogchul				172	
Bogoslof		914		1,109	
Akutan				1,130	
Akun				60	
Ugamak				1,635	1,386
Sea Lion Rock				nc	
Total		914		4,950	1,386
Western Gulf:					
Clubbing Rocks	725	1,419	1,394		
Pinnacle	615	2,013	2,748		
Chernabura	545	646	200		379
Atkins	2,750	4,538	2,093		1,046
Total	4,635	8,616	6,435		1,425
Central Gulf:					
Chowiet	4,670	5,485	3,207		1,731
Chirikof	1,573	1,649	1,913		1,476
Marmot	6,140	6,741	5,751		4,286
Sugarloaf	5,021	5,123	3,114		3,107
Total	17,404	18,998	13,985		10,600

[1]Calkins and Pitcher (text fn. 5), except for Seguam and Bogoslof Islands, which are from Fiscus et al. (1981).
[2]This study and Loughlin et al. (text fn. 7).

TABLE 4.—Counts of adult and juvenile northern sea lions at Ugamak Island, AK, mid-June 1969-86[1].

Rookery or haul	1969[2] Date	1969[2] Count	1977[3] Date	1977[3] Count	1985[4] Date	1985[4] Count	1986[4] Date	1986[4] Count
South								
Cone	6/20	400+	6/28	337	6/20	68	6/20	59
Eagle	6/18	1,000+	6/28	412	6/20	95	6/20	85
Ugamak Bay								
A1	6/19	639	6/20	148	6/20	139	6/20	133
A2	6/19	1,583	6/20	406	6/20	439	6/20	546
A3	6/19	257	6/20	27	6/20	3	6/20	35
A4	6/19	1,467	6/20	369	6/20	272	6/20	15
A5	6/12	720	6/28	364	6/20	361	6/20	336
Total south		6,066		2,063		1,377		1,209
North								
North Point								
N1	6/19	576	6/19	80	6/20	1	6/20	0
N2	6/19	262	6/19	56	6/20	9	6/20	15
N3	6/19	197	6/19	330	6/20	3	6/20	2
NE Point								
NE1	6/14	975	6/19	429	6/20	328	6/20	156
NE2	6/14	1,400	6/28	500	6/20	315	6/20	302
North haul	6/19	819	6/28	119	6/20	0	6/20	0
Total north		4,229		1,514		656		475
Grand total		10,295		3,577		2,033		1,684

[1]Excludes three sites not counted in all four years. Last day of counting in 1969 was 20 June, so this table is designed to provide comparable data from other years only, and will not match the maximal count for the year. Sites are identified using scheme developed by Fiscus (text fn. 12).
[2]From Fiscus (text fn. 12).
[3]From land counts, except counts from 28 June 1977, which were taken from aerial photographs (Withrow (text fn. 10)).
[4]This study.

Island has not declined equally at all sites (Table 4). Numbers on the south side of the island at Ugamak Bay declined until 1977, and then changed very little through 1985. However, in 1986 one south side site (A4) was abandoned by breeding females, whereas it had been occupied by over 400 in the previous year. Numbers at north side sites have declined through the present, with most sites there now

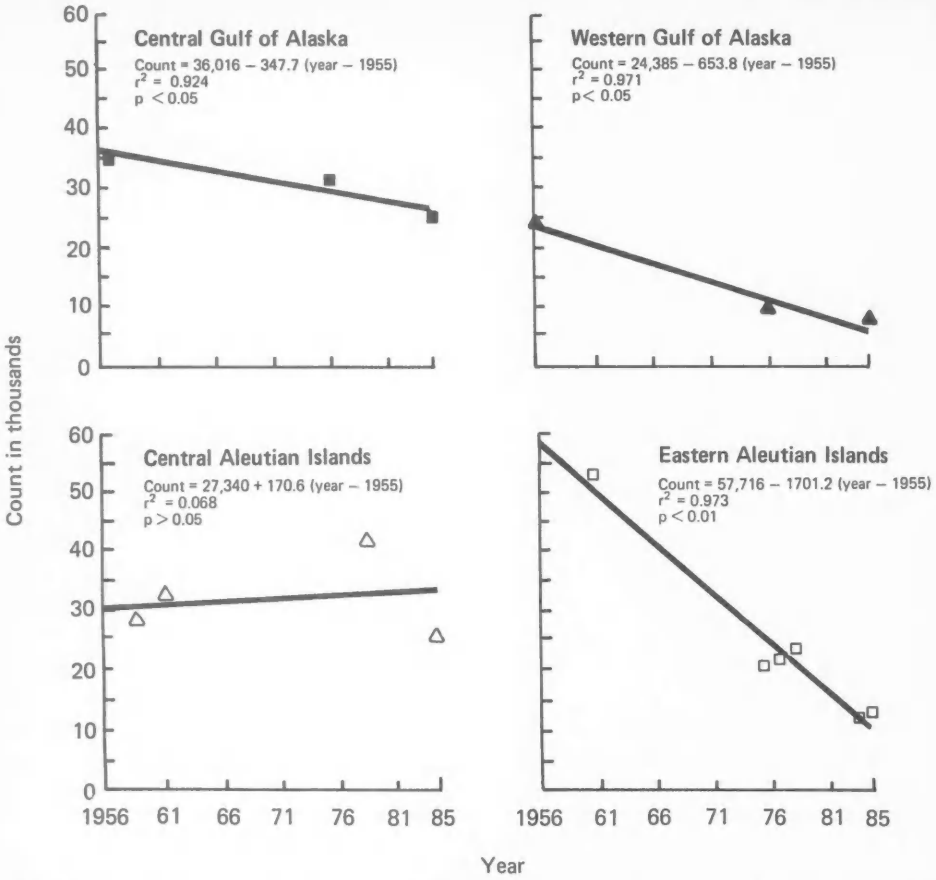

FIGURE 2.—Trends in total adult and juvenile northern sea lion abundance by area in Alaska, for spring and summer surveys conducted from 1956 to 1985.

empty. Although some rookeries have been reduced in size and decreases have been observed in all age and sex groups, the ratio of adult females to territorial males has remained relatively constant between 1977-78 (14.4-17.3) and 1986 (16.4). Between 1985 and 1986, however, the number of adult males remained constant, while the number of females decreased by 26%.

Island totals of juveniles were similar in 1985 (87 animals) and in 1986 (110 animals). However, an analysis of comparable areas of the island (i.e., N1-N3 and A2-A4; Fiscus[12]) indicated that the juvenile portion of the population had decreased significantly ($\chi^2 = 4.09$, $P < 0.05$) from 9.0% in 1977 to 1.4-1.6% in 1985-86. A comparably low rate (2%) has only been observed at Año Nuevo Island (Gentry 1970) and that rate was calculated for a single primary rookery rather than a whole island. Rates such as the 22% observed at Marmot Island in 1983 or the 25% observed for British Columbia in 1956 seem more typical for northern sea lion rookeries (Pike and Maxwell 1958; Merrick 1984).

Counts of pups were available for six rookeries

[12]Fiscus, C. H. 1970. Steller sea lions at Ugamak Island, Aleutian Islands, Alaska, June 1969. Unpubl. Rep., U.S. Fish Wildl. Serv., Bur. Commer. Fish., Mar. Mammal Biol. Lab., Seattle, 78 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

on the island for 1969, 1977, 1985, and 1986 (Fiscus fn. 12; Withrow fn. 10). The number of pups declined by 72% between 1969 and 1977, with two rookeries abandoned. A decline of 35% occurred between 1977 and 1986, with three more rookeries abandoned. Pupping has probably declined on other parts of the island, because the number of breeding animals decreased at other rookeries (Table 4) where pups were not counted in 1968 and 1977. Between 1985 and 1986, the only years with complete island surveys, there was a decline of 18% in pup numbers. Despite the decline in the number of pups born, the ratio of pups to adult females has increased from 0.75 in 1968 and 0.73-0.81 in 1977-78 to 0.95-1.06 in 1985-86. The Ugamak Island pup mortality during the first 1-2 mo postpartum in 1985-86 was 3.4-4.5%. Median pupping dates were similar in 1977-78 (13 June) and 1985 (12 June).

Finally, the Ugamak Island data allowed an evaluation of the times of peak abundance and variability in the counting methods. Counts peaked in 1985-86 between the third week of June and the first week of July, with 90% of the maximal breeding season population onshore at midday during this period. Hourly counts between 1000 and 2000 ADT during this period were always within 10% of the day's maximum. These occupancy patterns were the same as those observed by Withrow (1982) at Ugamak Island in 1977-78.

The Ugamak Island data also were used to provide an estimate of the accuracy of the 10 June 1985 aerial survey of the island. There was only a 3% difference between the aerial photo count and the simultaneous ground count. Thus, as noted by Withrow (1982), aerial photo counts accurately reflect ground counts. Despite this accuracy, the aerial photo count of 10 June 1985 was 24% lower than the maximal ground count of 25 June 1985. This bias was likely caused by the aerial survey occurring slightly before the period of peak abundance.

DISCUSSION

The number of northern sea lions found at sites within the study region, which included at least 140,000 animals circa 1958, totaled less than 68,000 in 1985—a decline of 52% (−2.7% per year). All indicators (regional numbers, breeding animals on rookeries, pup production, and the Ugamak Island data) confirm this decline. The rates of decline are probably underestimated because declines probably did not begin until after 1958. For example, the Ugamak Island population showed no decline between 1957 and 1969, and then declined at least 10.1% per year between 1969 and 1986. This indicates that the eastern Aleutian Island northern sea lion population may have begun to decline in the early 1970s rather than in 1958, the base year for rate calculations. Data are insufficient to calculate regional or area rates from 1969 to later dates.

Declines may have occurred in two phases. The first phase may have begun in the 1970s and been confined to the eastern Aleutian Islands and western Gulf of Alaska. Numbers for the entire study region fell by 25% (−1.6% per year) between 1958 and 1977. Numbers in the eastern Aleutian Islands appeared to stabilize in the mid-1970s, while those in the central Aleutian Islands and western Gulf of Alaska may have increased. A second phase of the decline may have begun during the late 1970s, with all areas being affected and overall numbers falling 36% (−5.2% per year) between 1977 and 1985. Results of the 1986 pup survey and 1986 Ugamak Island study indicate that the decline is still continuing.

Alternative Explanations for the Declines in Northern Sea Lion Numbers

Consideration has been given as to whether the declines could be explained by counting errors or biases, changes in northern sea lion behavior, or emigration. However, errors in counting or, for that matter, changes in technique do not explain the decline in numbers. Because counts taken in the 1950s and 1960s were conducted in the spring (before abundance had peaked on land) and because sites were missed, we believe that they underestimated sea lion numbers. Braham et al. (1980) estimated that only 42% of the eastern Aleutian Island sites were surveyed in 1957 (Mathisen and Lopp 1963). Animals present were probably accurately counted in the pre-1970 surveys because observers were all experienced. Kenyon and Rice (1961) compared their visual counts to concurrent aerial photos taken and found that their error was between 6 and 10%. Even if they had overestimated numbers the error may have been counterbalanced by any underestimate from counting too early in the year. The counts of the 1970s and 1980s were probably more comparable because they were made during the period of peak numbers onshore. Also there was little variation during this period in methods and personnel were experienced in these survey techniques. Furthermore, the methods used were believed to have been the most accurate. Even if all of the aerial counts were lower than the maximal

count for the season (as observed at Ugamak Island in 1985), the amount of error would be insufficient to explain the low counts. In any event, the declines in northern sea lion numbers observed in aerial surveys since the 1970s have been confirmed by the counts made from land at Ugamak Island and by the pup counts taken in the eastern Aleutian Islands and the Gulf of Alaska.

Pup counts can provide a reliable index of population change since almost all pups born can be counted in surveys scheduled prior to the pups going to sea. However, the index may be biased (Berkson and DeMaster 1985). Briefly stated, if precount pup survival (e.g., live birth rates) is density-dependent the counts would overestimate the rate of decline. If postcount pup survival (e.g., juvenile survival) is density-dependent then the counts would underestimate the rate of decline. Finally, if adult survival is density-dependent there would be little bias. Few data exist on density-dependent population regulation in northern sea lions, so we cannot be sure which, if any, of these mechanisms are operative. However, available data suggest that while precount survival in recent years is either unchanged or has improved, postcount survival has decreased. In both cases, the effect would be for pup counts to understate the rate of decline.

It is unclear whether northern sea lion hauling behavior has changed sufficiently to affect the counts. The 1977-78 and 1985-86 Ugamak Island data show that seasonal and daily hauling patterns and the timing of critical events (e.g., the median pupping date) have not changed. Similar data are not available for the earlier surveys. Animals may have dispersed to other sites, but they still would have been counted in the regional surveys. There is some evidence from Ugamak Island that females may spend less time ashore now than before (e.g., the high ratio of pups to adult females), which would decrease the number of adult animals counted. The low number of juveniles counted at Ugamak Island in 1985-86 may simply reflect increased juvenile dispersal away from the site due to changing prey resources and earlier weaning.

The decline in northern sea lion numbers onshore in the region has not been due to the emigration of animals to other regions because significant increases have not been noted elsewhere. Numerical decreases have been noted at the western extent of the breeding range in the Kuril and Commander Islands (Perlov 1982; Kuzin et al. 1984; Chelnokov 1984). Numbers began to fall in this region circa 1972, and by 1981-82 had fallen by 50% or more. Abundance at sites in the western Aleutian Islands declined 34-61% from 1979 to 1985 (Klett[13]). Adult northern sea lions at the Pribilof Islands have declined in number from approximately 7,000 animals in 1960 to 1,100 in 1981 (Kenyon 1962; Loughlin et al. 1984). Most of these animals were located at Walrus Island which was occupied by 4,000-5,000 northern sea lions in 1960, around 1,500 in 1975, and only 600 in 1982 (Kenyon 1962; NMML fn. 11). In 1960, 2,866 pups were counted at Walrus Island, but this number had fallen to 334 by 1982 (Kenyon 1962; NMML fn. 11). Northern sea lions are regularly seen farther north at St. Matthew and St. Lawrence Islands during the ice-free season, but the total has rarely exceeded 300 animals (Loughlin et al. 1984). Frost et al.[14] estimated 2,000 animals were in northern Bristol Bay during the 1970s, with 1,500 observed in the summers of 1980-82. The only rookery in Bristol Bay, Sea Lion Rock (Table 1), has decreased in size by 81% since the counts of 1957 reported by Mathisen and Lopp (1963). The 1982 count of 7,962 animals in southeast Alaska was not substantially different from the 1973 estimate of 8,430 (Calkins and Pitcher[15]). The number of northern sea lions in British Columbia and in the lower United States (i.e., Washington, Oregon, and California) do not appear to be increasing from 5,700 and 5,410 animals, respectively (Loughlin et al. 1984; Bigg 1985).

Proximate Causes of the Decline

The declines of northern sea lion could either be due to falling reproductive rates or reduced survival of pups, juveniles, and adults (especially females). There does not, however, appear to have been significant declines in reproductive rates or in pup survival 1-2 mo postpartum. The pregnancy rate of females taken in the Gulf of Alaska during April-May 1985 was 62% (n = 62), which was not significantly different from the 67% (n = 102) found there in 1975-78 (χ^2 = 0.002, $P > 0.50$; Pitcher and Calkins 1981; Goodwin and Calkins[16]). In addition,

[13]E. Klett, U.S. Fish and Wildlife Service, Aleutian Island Unit, Alaska Maritime National Wildlife Refuge, Box 5251 Naval Air Station, Adak, AK 98791, pers. comm. March 1986.

[14]Frost, K. J., L. F. Lowry, and J. J. Burns. 1982. Distribution of marine mammals in the coastal zone of the Bering Sea during summer and autumn. Alaska Dep. Fish Game, Final Rep. RU613, 188 p. Alaska Department of Fish and Game, 1400 College Road, Fairbanks, AK 99701.

[15]Calkins, D. G., and K. Pitcher. 1983. 1982 pinniped investigations in southern Alaska. Unpubl. rep., 15 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[16]Goodwin, E. A., and D. G. Calkins. 1985. Preliminary results of ongoing investigations of San Miguel Sea Lion Virus, Leptospirosis, and Chlamydiosis in Alaska Steller sea lions and their rela-

the ratio of pups to adult females at Ugamak Island has increased since 1968 and 1977-78. The 3.4-4.5% rate of pup mortality at Ugamak Island was low when compared with the 11% found at Marmot Island, 10% at Año Nuevo Island, CA, and the 13-14% at Wooded Island, AK (Gentry 1970; Sandegren 1970; Merrick 1984).

The declines of northern sea lion may be due to reduced survival of pups (after they go to sea), juveniles, and adults. Changes in survival rates are difficult to assess. The precipitous declines in pupping in the Gulf of Alaska (Table 3) may indicate that there have been large declines in the female population there. Numbers of adult females at Ugamak Island also declined between 1985 and 1986. The Ugamak Island data also seem to indicate that juvenile abundance was much lower in 1985-86 than at other sites and in other years, which may indicate unusually high mortality is occurring after pups leave the rookery. Investigation of the declines in juveniles and adult females may hold the greatest promise for further study.

Ultimate Causes of the Decline

The causes of the reduced fecundity or survival of northern sea lions are presently unknown, but there are several possibilities—disease, changes in prey resources, and the combined effects of these and other factors. Disease and prey limitations are particularly plausible causes of the decline because of their potential for widespread impacts (hence declines in other regions) and because they could be implicated in the apparent declines of other Bering Sea and North Pacific Ocean pinniped populations. The number of northern fur seals, *Callorhinus ursinus*, breeding at the Pribilof Islands and on Robben Island in the Sea of Okhotsk have decreased since the mid- to late 1970s (Fowler 1985). Since the 1970s, harbor seal, *Phoca vitulina richardsi*, numbers may have decreased in Bristol Bay (Pitcher[17]) and have declined substantially in the central Gulf of Alaska at Tugidak Island (Calkins and Pitcher[18]).

Diseases resulting in reproductive failures and neonate, juvenile, and adult mortality could be a significant source of mortality. Antibodies to two types of bacteria (*Leptospira* and *Chlamydia*) and one marine calicivirus virus (San Miguel Sea Lion Virus) which could produce such mortality were present in blood taken from northern sea lions in Alaska (Fay et al. 1978[19]; Goodwin and Calkins fn. 16; Barlough et al. in press). Leptospires are spirochete bacteria and are suspected agents of abortion and adult mortality in California sea lions, *Zalophus californianus*, (Smith et al. 1974a) and in northern fur seals (Smith et al. 1974b). San Miguel Sea Lion Virus may also be associated with reproductive failures or neonatal deaths in California sea lions and northern fur seals, although the evidence is limited (Smith et al. 1973). *Chlamydia* has not been studied previously in sea lions. These and other agents are being examined for their possible adverse effects on northern sea lion populations.

The decline in northern sea lion numbers may be related to changes in the quantity and size of their prey. The few studies of the food habits of northern sea lions indicated that their primary prey are walleye pollock, *Theragra chalcogramma*, in the Bering Sea, Gulf of Alaska, and North Pacific Ocean (Klumov 1957; Pitcher 1981; Calkins et al.[20]). This fish is also a major prey item of harbor seals and northern fur seals (Pitcher 1980; Kajimura 1984). Walleye pollock biomass in the eastern Bering Sea rose from less than 5 million metric tons (t) in the 1960s to a peak of over 13 million t in the early 1970s and has since declined to about 8 million t in 1985 (Bakkala et al. in press). While the population biomass remains high, sporadically low abundance of age-1 walleye pollock between 1979 and 1984 could mean that in some years (e.g., 1981, 1982, and 1984) there would be fewer fish in the 10-35 cm range (Bakkala et al. in press). This size range includes the mean sizes consumed by northern sea lions and harbor seals (Pitcher 1981; Frost and Lowry 1986). Declines in abundance and increases in fish length have also been noted since 1981 in the Shelikof Strait region of the Gulf of Alaska (Nelson and Nunnallee 1985). However, there are few data on northern sea lion foraging patterns in the Bering Sea and

tionship to declining pup counts. Presented at the Sixth Biennual Conference on Biology of Marine Mammals, Vancouver, B.C., Nov. 1985. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[17]K. Pitcher, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502, pers. comm. February 1986.

[18]Calkins, D. G., and K. Pitcher. 1985. Pinniped investigations in southern Alaska: 1983-84. Unpubl. rep., 19 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[19]Fay, F. H., R. A. Dieterich, L. M. Shults, and B. P. Kelley. 1978. Morbidity and mortality in marine mammals. U.S. Dep. Commer. and U.S. Dep. Inter. (OCSEAP), Environ. Assess. Alaska Cont. Shelf, Ann. Rep., Mar. 1978, 1:39-79.

[20]Calkins, D. G., G. A. Antonelis, Jr., and G. W. Oliver. 1981. Preliminary report of the Steller sea lion/ice seal research cruise of the *ZRS Zvyagino*. Unpubl. rep., 22 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

Gulf of Alaska, so a relationship between the declines in northern sea lion numbers and changes in the abundance of their prey cannot be rejected or confirmed.

The declines of northern sea lion may not have a single cause, but may be due to the effects of a combination of these and other factors. Sources of mortality which alone seem insufficient to account for the declines but which could be important in a combined effect include the pre-1973 commercial sea lion harvests, entanglement in marine debris, incidental taking in fisheries, and the killing of sea lions for bait and predator control.

Northern sea lions were commercially harvested in the eastern Aleutian Islands and Gulf of Alaska from 1959 to 1972. Six hundred and sixteen adult males were taken in an experimental harvest in 1959 (Thorsteinson et al. 1961). A total of 45,178 northern sea lion pups of both sexes were harvested in the eastern Aleutian Islands and Gulf of Alaska between 1963 and 1972 (FEIS[21]). The largest harvests were conducted between 1963 and 1972 at Sugarloaf and Marmot Islands where 16,763 and 14,180 pups, respectively, were killed, and between 1970 and 1972 at Ugamak and Akutan Islands where 3,773 and 6,036 pups, respectively, were killed. The pup harvests, which sometimes reached 50% of the total pup production from a rookery (e.g., at Sugarloaf Island in 1965 and 1968), could have depressed recruitment in the short term. This may partially explain the declines experienced at some sites through the mid-1970s. However, it is unclear why numbers declined in areas where no harvest occurred (e.g., the north side of Ugamak Island), while no declines were observed at some harvest sites (e.g., Marmot Island). In any event, those harvests should not currently be affecting the decline, because populations should have stabilized 3-5 years after the cessation of harvesting as unharvested year classes reached breeding age. Furthermore, these harvests probably cannot explain the declines in numbers counted in the western and central Aleutian Island populations.

Little information exists on the effect of entanglement in marine debris on northern sea lions. Despite debris commonly being found in areas northern sea lions frequent (Calkins 1985; Merrell 1985), data from NMML surveys suggest that this is not a problem, at least for adult sea lions. Observed entanglement rates were 0.07% in the 1985 ship survey (Loughlin et al. fn. 7), 0.09-0.17% in the 1985-86 Ugamak Island surveys, and 0.12% at Marmot Island in 1983 (Merrick 1984). Numerous northern sea lion pups were seen in the November 1985 eastern Aleutian Island entanglement survey (Loughlin et al. fn. 7), but none were entangled. Nevertheless, it is possible that entangled northern sea lion pups drown and are not observed.

Numerous northern sea lions have been taken incidental to fisheries in the Bering Sea and Northeast Pacific Ocean since the late 1960s and early 1970s (FEIS fn. 21). In 1978-81 the estimated average annual mortality for all foreign vessels was 724 animals (Loughlin et al. 1983). This does not, however, include animals taken by U.S. fishermen fishing in joint ventures or independently. Loughlin and Nelson (1986) documented the take in the Shelikof Strait joint venture walleye pollock fishery where an estimated 958 to 1,436 northern sea lions were caught by U.S. trawlers in 1982. This take declined to less than 400 animals per season in 1983 and 1984, probably due to changes in fishing technique and the area and times fished. The cumulative impact of foreign independent and joint venture fisheries in the Bering Sea and North Pacific Ocean probably now accounts for less than 500 deaths per year (NMML fn. 11). Domestic fishermen now working independently probably take less since they generally are involved in fisheries that catch few sea lions. However, as foreign fishing is phased out of U.S. waters, the domestic take will probably increase. The foreign and domestic incidental take contributes to but cannot totally account for the decline.

We are uncertain how the killing of northern sea lions by fishermen has affected the population. Fishermen have been observed to kill adult animals at rookeries, haul-outs, and in the water near boats, but the magnitude of this take is generally unknown. Trawl fisheries attract many northern sea lions during haulback operations and shooting at these animals is a common occurrence. One of the few estimates of shooting mortality comes from Matkin and Fay[22] who calculated that 305 northern sea lions were killed directly (shot) while interferring with fishing operations in the spring 1978 Copper River Delta salmon gill net fishery. Northern sea lions at

[21]Final environmental impact statement (FEIS). 1977. Consideration of a waiver of the moratorium and return of management of certain marine mammals to the State of Alaska. Vol. II. U.S. Dep. Commer. and U.S. Dep. Inter., Interagency Task Group, Wash., D.C., 251 p.

[22]Matkin, C. O., and F. H. Fay. 1980. Marine mammal-fishery interactions on the Copper River and in Prince William Sound, Alaska, 1978. Final rep. for contract MMC-78/07 to Mar. Mammal Comm., 71 p. Available from National Technical Information Service, U.S. Department of Commerce, Springfield, VA 22161, as PB80-159536.

sites in the eastern Aleutian Islands also would have been prime sources of bait for crab fishermen. Thus it may be more than a coincidence that the onset of the northern sea lion decline in the eastern Aleutian Islands began at the time of peak landings in the Bering Sea king crab (*Paralithodes* spp., *Lithodes aequispina*) and Tanner (snow) crab (*Chionoecetes* spp.) fisheries. Killing "nuisance" northern sea lions continues to this date (R. L. Merrick pers. obs.). This killing may have a significant effect on local populations (e.g., the eastern Aleutian Islands and central Gulf of Alaska) and might have caused animals to disperse away from traditional rookeries and haul-outs. It should have little effect, however, in areas that have not been heavily fished (e.g., the western and central Aleutian Islands).

Sources of mortality that we think are of minor or unknown importance in the decline include changes in oceanographic or climatic conditions, increased predation, harassment, subsistence harvests, and chemical pollutants.

Prospects for the Future

Many pinniped species have experienced population declines within recent history, and in most cases the population has been able to rebuild. Overexploitation has been a cause of long-term but temporary declines in many species, including Southern Hemisphere fur seals (*Arctocephalus* spp.), elephant seals (*Mirounga* spp.), and northern fur seals (Bonner 1982). Other human activities have caused declines, such as that of ringed seals, *Phoca hispida*, in the Baltic Sea, where organochlorines may have caused a high rate of reproductive failures (Helle et al. 1976). Natural mortality and temporary local declines have resulted from influenza outbreaks in northwest Atlantic Ocean harbor seals, *Phoca vitulina concolor*, (Geraci et al. 1983), and Leptospirosis epizootics in California sea lions (Vedros et al. 1971). Decreased prey abundance may have reduced the ringed seal and bearded seal, *Erignathus barbatus*, populations in the eastern Beaufort Sea in 1974-75 (Stirling et al. 1982).

Thus the northern sea lion decline in southwestern Alaska is not unique among pinnipeds, but the causative factor remains difficult to identify. Based on these other examples we can estimate what the ultimate effect of the most plausible hypotheses will be on the population. If one of the causes of the decline is disease, then the population will stabilize and begin to increase once the epizootic has run its course. If a change in prey quantity or quality has reduced the carrying capacity of the Bering Sea, Gulf of Alaska, and North Pacific Ocean for northern sea lions, then the population should stabilize if the critical resource stabilizes. If the decline is caused by a combination of factors, then the outcome cannot be determined. Though serious, the current reduced status of the stock in southwestern Alaska does not yet imperil the population, because a large reservoir of adult breeding animals remains to rebuild the population should the decline abate.

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LITERATURE CITED

BAKKALA, R., V. WESPESTAD, AND L. L. LOW.
In press. Historical trends in abundance and current condition of walleye pollock in the eastern Bering Sea. Fish. Res.

BARLOUGH, J. E., E. S. BERRY, E. A. GOODWIN, R. F. BROWN, R. L. DELONG, AND A. W. SMITH.
In press. Antibodies to marine caliciviruses in the Steller sea lion (*Eumetopias jubatus* Schreber). J. Wildl. Dis.

BERKSON, J. M., AND D. P. DEMASTER.
1985. Use of pup counts in indexing population changes in pinnipeds. Can. J. Fish. Aquat. Sci. 42:873-879.

BIGG, M. A.
1985. Status of the Steller sea lion (*Eumetopias jubatus*) and California sea lion (*Zalophus californianus*) in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci. 77, 20 p.

BONNER, W. N.
1982. Seals and man: A study of interactions. Univ. Wash. Press, Seattle, 170 p.

BRAHAM, H. W., R. D. EVERITT, AND D. J. RUGH.
1980. Northern sea lion population decline in the eastern Aleutian Islands. J. Wildl. Manage. 44:25-33.

CALKINS, D. G.
1985. Steller sea lion entanglement in marine debris. *In* R. S. Shomura and H. O. Yoshida (editors), Proceedings of the Workshop on the Fate and Impact of Marine Debris 27-29 November 1984, Honolulu, Hawaii, p. 308-314. U.S. Dep. Commer., NOAA Tech. Memo. NMFS SWFC-54.

CHELNOKOV, F. G.
1984. Abundance of sea lions and their relationship with fur seals at the southeastern hauling ground of Mednyi Island (Commander Islands). Sov. J. Mar. Biol. 9:191-195. [Engl. transl. Biol. Morya.]

FISCUS, C. H., D. J. RUGH, AND T. R. LOUGHLIN.
1981. Census of northern sea lion (*Eumetopias jubatus*) in central Aleutian Islands, Alaska, 17 June-15 June 1979, with notes on other marine mammals and birds. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS F/NWC-17, 109 p.

FOWLER, C. W.
1985. An evaluation of the role of entanglement in the population dynamics of northern fur seals on the Pribilof Islands. *In* R. S. Shomura and H. O. Yoshida (editors), Proceedings of the Workshop on the Fate and Impact of Marine Debris 27-29 November 1984, Honolulu, Hawaii, p. 291-307. U.S. Dep. Commer., NOAA Tech. Memo. NMFS SWFC-54.

FROST, K. J., AND L. F. LOWRY.
1986. Sizes of walleye pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea. Fish. Bull., U.S. 84:192-197.

GENTRY, R. L.
1970. Social behavior of the Steller sea lion. Ph.D. Thesis, Univ. California, Santa Cruz, 113 p.

GERACI, J. R., D. J. ST. AUBIN, I. K. BARKER, R. G. WEBSTER, V. S. HINSHAW, W. J. BEAN, H. L. RUNHKE, J. H. PRESCOTT, G. EARLY, A. S. BAKER, S. MADOFF, AND R. T. SCHOOLEY.
1982. Mass mortality of harbor seals: pneumonia associated with influenza A virus. Science (Wash., D.C.) 215:1129-1131.

HELLE, E., M. OLSSON, AND S. JENSEN.
1976. DDT and PCB levels and reproduction in ringed seal from the Bothnian Bay. Ambio 1976, p. 188-189.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. John Wiley & Sons, N.Y., 503 p.

KAJIMURA, H.
1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-779, 49 p.

KENYON, K. W.
1962. History of the Steller sea lion at the Pribilof Islands, Alaska. J. Mammal. 43:68-75.

KENYON, K. W., AND D. W. RICE.
1961. Abundance and distribution of the Steller sea lion. J. Mammal. 42:223-234.

KLUMOV, S. K.
1957. Registration of the shore rookeries of sea lions (*Eumetopias jubatus*) in the Kuril Islands and tentative determination of their numerical magnitude. [In Russ.] Dokl. Akad. Nauk. SSSR 117(2):345-348. (Transl. L. V. Sagen, avail. Natl. Mar. Mammal Lab. Library.)

KUZIN, A. E., M. K. MAMINOV, AND A. S. PERLOV.
1984. The number of pinnipeds and sea otters on the Kuril Islands. *In* V. E. Rodin, A. S. Perlov, A. A. Berzin, G. M. Gavrilov, A. I. Shevchenko, N. S. Fadeev, and E. B. Kucheriavenko (editors), Marine mammals of the Far East, p. 54-72. [In Russ.] Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO), Vladivostok. (Transl. F. H. Fay., avail. Natl. Mar. Mammal Lab. Library.)

LOUGHLIN, T. R., L. CONSIGLIERI, R. L. DELONG, AND A. T. ACTOR.
1983. Incidental catch of marine mammals by foreign fishing vessels, 1978-81. Mar. Fish. Rev. 45(7-8-9):44-49.

LOUGHLIN, T. R., D. J. RUGH, AND C. H. FISCUS.
1984. Northern sea lion distribution and abundance: 1956-80. J. Wildl. Manage. 48:729-740.

LOUGHLIN, T. R., AND R. NELSON, JR.
1986. Incidental mortality of northern sea lions in Shelikof Strait, Alaska. Mar. Mammal Sci. 2:14-33.

MATHISEN, O. A., AND R. J. LOPP.
1963. Photographic census of the Steller sea lion herds in Alaska, 1956-58. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 424, 20 p.

MERRELL, T. R., JR.
1985. Fish nets and other plastic litter on Alaska beaches. *In* R. S. Shomura and H. O. Yoshida (editors), Proceedings of the Workshop on the Fate and Impact of Marine Debris 27-29 November 1984, Honolulu, Hawaii, p. 160-182. U.S. Dep. Commer., NOAA Tech. Memo., NMFS SWFC-54.

MERRICK, R. L.
1984. Observations on the status of the northern sea lion population in Alaska. M.S. Thesis, Oregon State Univ., Corvallis, 85 p.

NELSON, M. O., AND E. P. NUNNALLEE.
1985. Acoustic-midwater trawl survey of spawning walleye pollock in the Shelikof Strait Region, 1980-81 and 1983-84. *In* R. L. Major (editor), Condition of ground fish resources of the Gulf of Alaska region as assessed in 1984, p. 179-206. U.S. Dep. Commer., NOAA Tech. Memo., NMFS F/NWC-80.

PERLOV, A. S.
1982. Reduction in the number of sea lions. [In Russ.] *In* G. B. Agarkov, V. A. Arsen'ev, V. M. Bel'kovich, V. A. Zemskiyi, L. A. Popov, I. V. Smelova, A. S. Sokolov, A. G. Tomlin, and A. K. Yablokov (editors), The study, preservation, and rational exploitation of marine mammals, p. 284-285. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr., Akad. Nauk. SSSR, Astrakhan. (Transl. by S. Pearson, Natl. Mar. Mammal Lab., NMFS, NWAFC, Seattle.)

PIKE, G. C., AND B. E. MAXWELL.
1958. The abundance and distribution of the northern sea lion (*Eumetopias jubata*) on the coast of British Columbia. J. Fish. Res. Board Can. 15:5-17.

PITCHER, K. W.
1980. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Fish. Bull., U.S. 78:544-549.
1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull., U.S. 79:467-472.

PITCHER, K. W., AND D. G. CALKINS.
1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. J. Mammal. 62:599-605.

SANDEGREN, F. E.
1970. Breeding and maternal behavior of the Steller sea lion (*Eumetopias jubata*) in Alaska. M.S. Thesis, Univ. Alaska, College, AK, 138 p.

SMITH, A. W., S. H. MADIN, AND T. G. AKERS.
1973. Pinnipeds as a possible natural reservoir for a virus

disease of domestic swine. Proceedings of the 10th Annual Conference of the Biological Sonar and Diving Mammals, Stanford Research Inst., Menlo Park, CA.

SMITH, A. W., R. J. BROWN, D. E. SKILLING, AND R. L. DELONG.
1974a. *Leptospira pomona* and reproductive failure in California sea lions. J. Am. Vet. Med. Assoc. 165:996-998.

SMITH, A. W., C. M. PRATO, W. G. GILMARTIN, R. J. BROWN, AND M. C. KEYES.
1974b. A preliminary report on potentially pathogenic microbiological agents recently isolated from pinnipeds. J. Wild. Dis. 10:54-59.

STIRLING, I., M. KINGSLEY, AND W. CALVERT.
1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974-79. Can. Wildl. Serv., Occas. Pap. 47, 25 p.

THORSTEINSON, F. V., R. W. NELSON, AND D. F. LALL.
1961. Experimental harvest of the Steller sea lion in Alaska waters. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 371, 15 p.

VEDROS, N. A., A. W. SMITH, J. SCHONEWALD, G. MIGAKI, AND R. C. HUBBARD.
1971. Leptospirosis epizootic among California sea lions. Science (Wash., D.C.) 172:1250-1251.

WITHROW, D. E.
1982. Using aerial surveys, ground truth methodology, and haul out behavior to census Steller sea lions, *Eumetopias jubatus*. M.S. Thesis, Univ. Washington, Seattle, 102 p.

ON THE ESTIMATION OF NUMBERS OF NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, PUPS BORN ON ST. PAUL ISLAND, 1980-86

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ABSTRACT

Since 1962, the numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island have been determined using a mark-recapture procedure. We investigate the feasibility of determining estimates of the total pup population on the 14 rookeries of St. Paul Island from subsamples of rookeries. Estimates are derived from simple random sampling and stratified (by rookery size) random sampling using standard ("blow up") estimation procedure, and ratio and regression estimates (based on the same sampling procedure but taking advantage of a strong relationship between numbers of breeding males and live pups on the various rookeries). Evaluation of the sampling schemes and estimation methods is based on the performance of the estimators for 3 years (1965, 1970, 1975) of data for which the mark-recapture estimates from all 14 rookeries were available. Ratio estimates are preferred to estimates obtained from the standard procedure for both simple random sampling and stratified random sampling. Furthermore, estimates from sampling plans based on three strata proved more satisfactory than those based on either unstratified or two-strata sampling. The ratio methods are applied to data collected during 1980-86. The number of northern fur seal pups born on St. Paul Island decreased at approximately 7.5% per year during 1975-81. There was no statistically detectable trend in numbers born during 1981-86.

The number of northern fur seals, *Callorhinus ursinus*, born on St. Paul Island (approximately 80% of the total Pribilof Islands herd production) has been determined in a variety of ways since the United States assumed direct management of the fur seal herd in 1910 (Parker 1946). The history of northern fur seal population estimation during 1912-47 and analyses of the reliability of methods then proposed for estimating numbers of pups are presented in Kenyon et al. (1954). The evolution of the "shearing-sampling" method, a variant of the mark-recapture technique, is discussed in Chapman (1964) and Chapman and Johnson (1968).

Since 1962, the estimate of the size of the pup population has been obtained using the "shearing-sampling" method. The safety of the crew, the accuracy of the estimate, and the minimization of disturbance to rookeries are major concerns; hence, the work is done as the breeding structure breaks up, but before pups spend most of their time in the water. During early August, a large number of pups (approximately 10% of the population) are marked by shearing a small patch of hair from the top of their heads; this exposes the pale underfur and produces an easily identifiable mark. The marking effort is allocated throughout the rookery so that each pup has an approximately equal chance of being marked. A few days later, each rookery is sampled twice during different periods to estimate the proportion of marked animals on the rookery. Thus, estimates of the population size and its variance can be calculated for each rookery. The estimate of the population present at the time of shearing is the number of sheared animals divided by the proportion of sheared pups among all those resighted—the normal Petersen estimate. The variance of this estimate is one-fourth the squared difference of the two estimates.

The purpose of this paper is to demonstrate the feasibility of obtaining accurate estimates of the total pup population on St. Paul Island from "shearing-sampling" estimates on a few sample rookeries. The advantages of obtaining estimates of the population from a subsample of rookeries include 1) less disturbance on the total northern fur seal population (each season that pup production is estimated on a particular rookery, crews must traverse the rookery four times—once to do the marking, twice to estimate the proportion of marked pups among the population, and once to count the number of dead pups); and 2) considerable savings in time, energy, and funds.

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METHODS AND AVAILABLE DATA

The data (Table 1) used for evaluating procedures for estimating the size of the pup population on St. Paul Island were the counts of breeding males made in mid-July and the estimate of the size of the pup population made in early August.

We assumed that for any year, the sum of the estimated numbers of live pups from each of the 14 rookeries, T, was the known or "true" size of the population. Estimates of the variances σ^2 each rookery were available; we assumed that the counts from each rookery were independent and estimated the variance of the total population, σ^2, as the sum of the estimated variances on the 14 rookeries. An approximate 95% confidence interval for the total population was $T \pm t(0.975,14)\,\sigma$, where $t(0.975,14)$ is the 97.5 percentile of Student's t distribution with 14 degrees of freedom.

Two sampling schemes and three estimation procedures were investigated. In particular, estimates based on the standard procedure or the "blow-up" estimate, were compared with ratio and regression estimates, which take advantage of a strong correlation between the numbers of breeding bulls and numbers of pups on the rookeries (Figs. 1, 2); these estimation procedures were compared under both simple random sampling and stratified random sampling schemes. For each sampling scheme, all possible subsamples of the 14 rookeries were generated, and the distributions of estimates for each of the 3 years of data were constructed. To determine how well the estimates predict the "true" population, we computed the fraction of (nominal) 95% confidence intervals about the estimate which contained the "true" value (the actual confidence level of the 95% confidence region). In addition, we computed the variance, bias, and the average half-width of the nominal 95% confidence interval of each estimator under the given sampling design.

"Blow-up" estimates of the total numbers of pups on the rookeries under simple random sampling, T_{BU}, were calculated in the following way (Cochran 1977): Let $(P_1, P_2, \ldots P_n)$ be estimates of pup numbers on n sample rookeries. The total on all rookeries was approximated by multiplying the average number of pups on the sample rookeries by the total number of rookeries:

$$T_{BU} = \frac{14}{n} \sum_{i=1}^{n} P_i = 14\,\bar{P}. \qquad (1)$$

The estimate of the variance of this estimate is

$$\mathrm{Var}(T_{BU}) = \frac{14 - n}{n} \frac{14}{n(n-1)} \sum_{i=1}^{n} (P_i - \bar{P})^2 + \frac{14}{n} \sum_{i=1}^{n} \mathrm{Var}(P_i). \qquad (2)$$

When sampling was stratified, the above procedure was applied to each stratum. The total number of pups on all rookeries was estimated as the sum of the estimates on all strata; the variance was approximated by applying Equation (2) to each stratum and then summing over the strata.

Other methods of estimating the total number of pups on all rookeries, when a total count of breeding males was available, were suggested through an examination of the regression equations of numbers

TABLE 1.—Numbers of northern fur seal pups counted and their standard deviations, numbers of breeding bulls, and ratio of pups counted to breeding males for the rookeries of St. Paul Island, AK for 1965, 1970, and 1975.

	1965				1970				1975			
Rookery	Pups	SD	Bulls	Ratio	Pups	SD	Bulls	Ratio	Pups	SD	Bulls	Ratio
Vostochni	34,208.0	2,091.6	1,434	23.9	33,808.5	4,797.7	791	42.7	41,356.0	2,300.9	799	51.8
Tolstoi	25,122.0	294.2	876	28.7	22,194.0	1,759.3	570	38.9	31,107.5	1,375.3	621	50.1
Zapadni	25,066.0	4,228.5	978	25.6	33,665.5	1,112.3	664	50.7	36,815.5	4,413.1	610	60.4
Reef	29,032.5	488.6	1,179	24.6	24,907.0	4,464.7	716	34.8	27,561.0	1,050.8	622	44.3
Morjori	15,434.5	204.4	739	20.9	14,894.0	3,624.6	352	42.3	21,284.5	3,926.6	376	56.6
Polovina Cl.	18,547.5	491.4	650	28.5	17,092.5	1,880.2	390	43.8	24,869.5	4,017.1	461	53.9
L. Zapadni	14,306.0	1,937.5	551	26.0	15,240.0	739.6	325	46.9	21,168.0	2,115.7	363	58.3
Kitovi	11,361.0	244.7	486	23.4	12,713.0	1,678.7	241	52.8	12,965.0	2,511.0	267	48.6
Gorbatch	16,929.0	1,347.7	674	25.1	15,027.5	1,248.0	385	39.0	17,038.5	761.6	387	44.0
Ardiguen	2,680.5	997.7	105	25.5	3,106.5	77.1	108	28.8	2,774.0	297.0	85	32.6
Lukanin	5,290.0	895.2	204	25.9	5,508.5	1,608.7	107	51.5	5,704.0	868.3	112	50.9
Zapadni Reef	5,259.0	58.0	221	23.8	4,191.5	560.7	106	39.5	7,223.0	657.6	139	52.0
Polovina	5,291.0	2,426.8	220	24.1	3,707.5	222.7	87	42.6	4,354.5	1,130.7	88	49.5
L. Polovina	6,117.5	236.9	236	25.9	3,848.0	257.4	103	37.4	3,415.0	43.8	88	38.8
	214,644.5	6,019.9	8,553	25.1	209,904.0	8,479.6	4,945	42.4	257,636.0	8,558.0	5,018	51.3

of pups as a function of numbers of breeding males (Figs. 1, 2). The analyses of variance of these regressions indicated that the quality of the fits was excellent and that the relationship might be used for predictive purposes. No intercepts, except that for 1916 data, were significantly ($P > 0.95$) different from 0. We were interested in subsampling the rookeries (possibly conducting the estimation on as few as four rookeries) and therefore, if a regression estimator were to be used, it was desirable to reduce the number of parameters as much as possible. Inasmuch as the intercepts were not different from 0, the simpler model with no intercept was considered appropriate. Since the variance of the pup estimates was not constant for each rookery, weighting appeared necessary. The variance of the estimates of pup numbers was roughly proportional to the number of bulls, and in such cases (Draper and Smith 1966), the best estimate of the slope of regression line is the average number of pups divided by the average number of bulls (equivalent to the ratio of the total number of pups to the total number of bulls). In this case, the total number of pups on all rookeries was estimated in the following manner: Let $P_1, \ldots, P_n$ and $B_1, \ldots, B_n$ be as above, and B a count of the total number of bulls on all rookeries. Then the total number of pups on all rookeries may be estimated as

$$T_R = \frac{B \sum_{i=1}^{n} P_i}{\sum_{i=1}^{n} B_i} = r\,B. \qquad (3)$$

One estimate of the variance of this ratio estimator is

$$\mathrm{Var}\,(T_R) = \frac{B^2}{\left(\sum_{i=1}^{n} B_i\right)^2} \sum_{i=1}^{n} \mathrm{Var}(P_i)$$

(Cochran 1977). (4)

When stratified random sampling was used instead of simple random sampling, we calculated the estimator in the same way since the ratio of pups to breeding males did not vary significantly between strata. The difference was due to the evaluation procedures; the number of logical sampling combinations differed and the analysis was restricted to those combinations of sample rookeries that were consistent with the sampling design (e.g., one small rookery, one medium-sized rookery, and two large rookeries).

Another way to estimate the ratio and its variance is with jackknife methods (Mosteller and Tukey 1977). Let r_{-i} be the ratio of pups to breeding males on all but the i^{th} rookery, and r the ratio of pups to breeding males on all the sample rookeries (as in Equation (5)):

$$r_{-1} = \frac{\sum_{i=1}^{n} (n\bar{P} - P_i)}{\sum_{i=1}^{n} (n\bar{B} - B_i)}. \qquad (5)$$

Then, the i^{th} pseudovalue is $r_i^* = nr - (n-1)\,r_{-i}$. The jackknife estimate of the ratio, r^*, is the mean of the r_i^*'s and the variance of r^* is (Mosteller and Tukey 1977):

$$\mathrm{Var}(r^*) = \frac{\sum_{i=1}^{n} (r_i^* - r^*)^2}{n\,(n-1)}.$$

Thus, the jackknife estimate of the total numbers of pups on all rookeries, T_j, is

$$T_j = r^*\,B, \text{ and } \mathrm{Var}(T_j) = B^2\,\mathrm{Var}(r^*).$$

The advantage of the jackknife estimate over the ordinary ratio estimate is the reduction of bias and a simple method of calculating the variance.

The ordinary regression estimate (assuming that the intercept is 0) of the ratio of pups to bulls is

$$s = \frac{\sum_{i=1}^{n} P_i\,B_i}{\sum_{i=1}^{n} (B_i)^2}.$$

Thus, the regression estimator of total numbers of pups is

$$T_{Rg} = sB \text{ and } \mathrm{Var}(T_{Rg}) = B^2\,\mathrm{Var}(s).$$

The estimate of the variance of s is calculated from the mean square residual of the regression equation.

RESULTS

Regressions of numbers of northern fur seal pups

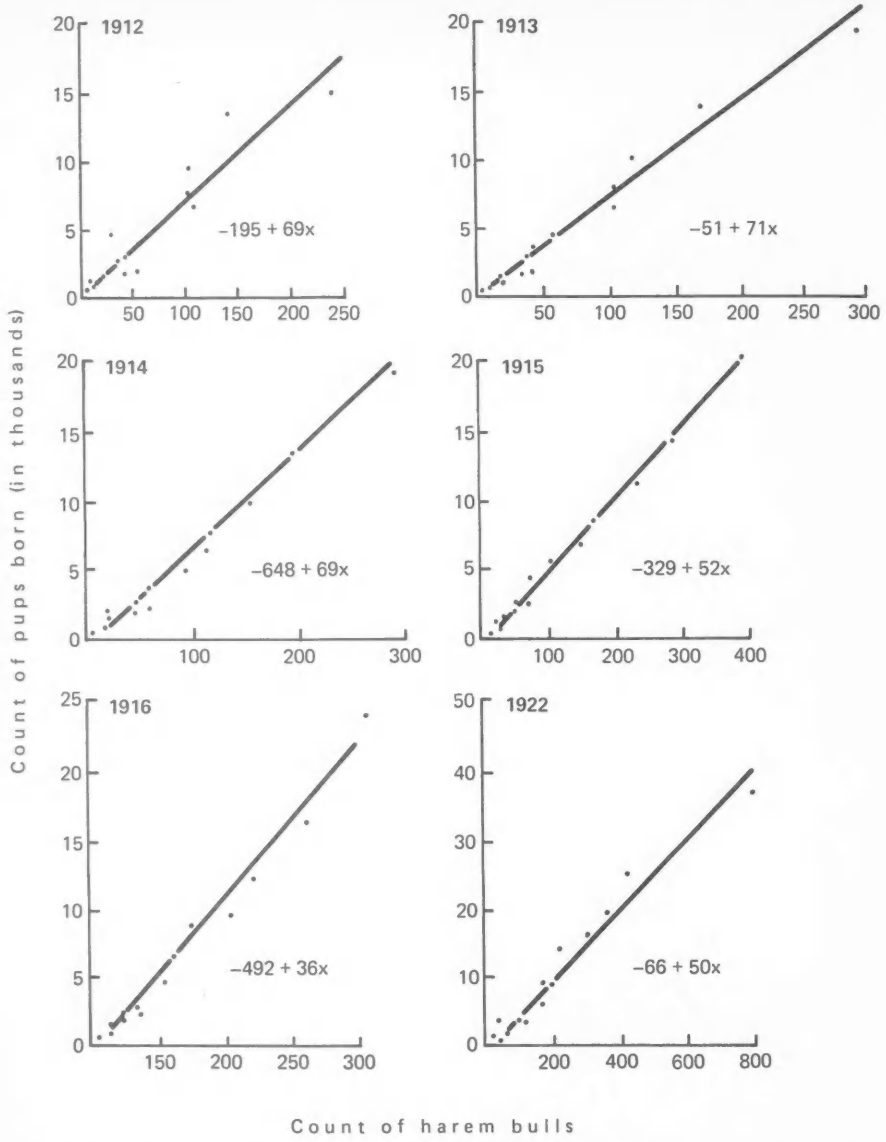

FIGURE 1.—Relationship of counts of northern fur seal pups born to counts of harem bulls for the various rookeries of St. Paul Island, AK, during 1912-22 (data from Lander 1980).

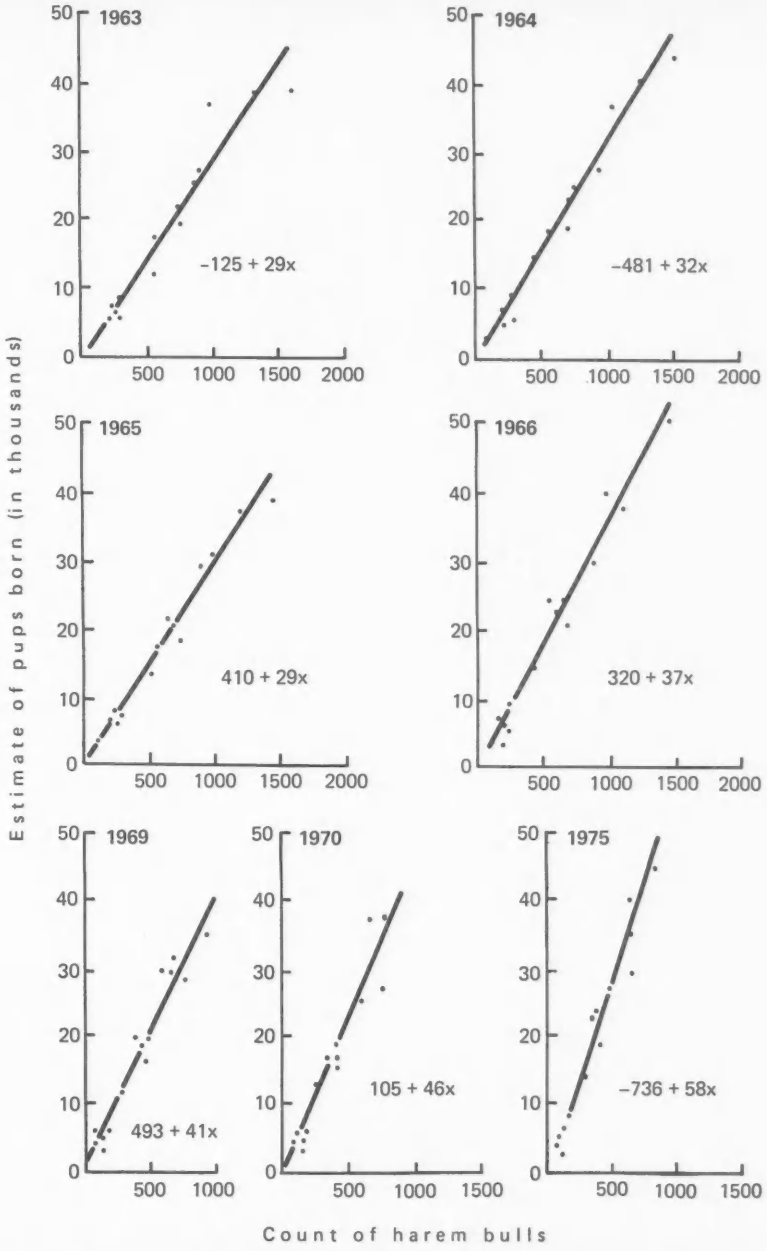

FIGURE 2.—Relationship of estimates of northern fur seal pups born and counts of harem bulls for the various rookeries of St. Paul Island, AK, during 1963-75 (data from Lander 1980).

versus numbers of breeding males for those years in which data were collected on all rookies indicated a strong relationship that could be used for prediction of total pup production if only subsamples of rookeries were censused. The relationship held for those years when censuses of pups were conducted by counting (Fig. 1), and for later years when the shearing-sampling method was used (Fig. 2). Although the slopes varied substantially from year to year (they ranged from 71 in 1913 to 29 in 1963), the variance about the regression line within any particular year was very small.

We compared the various estimators and sampling plans by analyzing the bias and variance of the estimates and the half-width and coverage properties of nominal 95% confidence intervals for 3 years (1965, 1970, 1975) of data when all rookies were sampled. Detailed statistics on the performance of the estimators under all sampling plans appear in a manuscript report available from the authors[3].

Under simple random sampling, the "blow-up" estimate is unbiased. The various ratio estimates are all slightly biased (in most cases less than 1%) with the regression estimate exhibiting the largest degree of bias. In Figure 3 the percentage of bias of the three ratio estimates for the 1975 data is shown as a function of sample size (under simple random sampling). Estimates based on 1975 data were the most biased among the 3 years analyzed, and these biases are exhibited as a worst case. The regression estimate was the most biased, and for these data the bias increased as the sample size increased; however, the bias was only about 1% and is not serious.

Confidence intervals were constructed for each subsample and a count was made of the number of nominal 95% confidence intervals containing the "true" population. The observed coverage was near 95% for most procedures. Confidence intervals for the regression estimate tended to be conservative, i.e., a higher than 95% coverage rate, while the coverage rate for the ordinary ratio estimate tended to be less than 95%. Coverage rates for the jackknife and blow-up estimates were near 95% or a bit higher. This indicates that the estimate of the variance of the regression estimate tended to be too large, that of the ordinary ratio estimate was too small, and that the estimates of the variance of the blow-up and jackknife estimates tended to be unbiased. The half-widths of confidence intervals for the ratio estimates were nearly equal. All were less than one-half the length of the half-width of the confidence interval of the blow-up estimate.

The rookeries were stratified by population size. Two methods for stratifying the rookeries were investigated: one using two strata (small and large rookeries) and the other using three strata (small, medium, and large rookeries). As in the case of simple random sampling, the ratio estimators were superior to the blow-up estimates. The estimators under the three-strata sampling plans were less variable than under the two-strata sampling plans. In addition, the computed levels of the nominal 95% confidence intervals were higher and the size of the confidence intervals smaller. Under the three-strata sampling plans, the standard deviations of the estimates were about 10% smaller than under simple random sampling with the same size sample. This resulted in a similar reduction in the size of the confidence intervals. These results indicated that reasonable estimates of the size of the pup population can be made using any of the ratio estimators under various sampling plans. The superior plans use three strata: two small, one medium, and one large rookery; one small, two medium, and one large

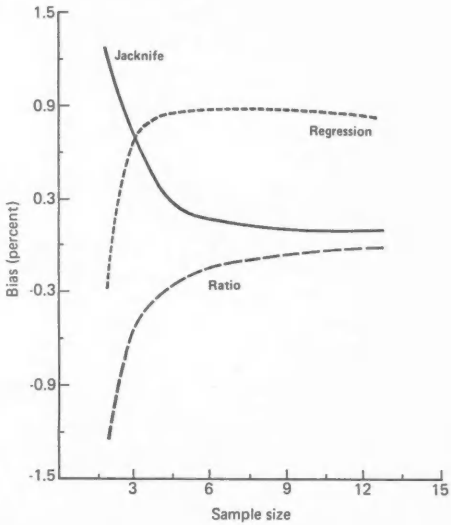

FIGURE 3.—Percent bias of the jackknife estimates (____), ordinary ratio estimates (· · ·), and regression estimates (----) based on simple random sampling of 1975 northern fur seal data.

[3]York, A. E., and P. Kozloff. 1985. Estimation of numbers of fur seal pups born on St. Paul Island, 1980-84. Unpubl. manuscr. Available National Marine Mammal Laboratory; 7600 Sand Point Way N.E., Seattle, WA 98115. (Background paper submitted to the 28th Annual Meeting of the Standing Scientific Subcommittee of the North Pacific Fur Seal Commission, March-April 1985, Tokyo, Japan.)

rookery; and, one small, one medium, and two large rookeries.

A subsampling estimation procedure was developed for 1980-84: rookeries were grouped into three strata—large, medium, and small rookeries; one small, one medium, and two large rookeries were sampled each year. Furthermore, in order that some rookeries were not disturbed inordinately more than others, each rookery was sampled at least once, but no more than twice during the 5-yr period. We had intended to census all rookeries in 1985, but logistic difficulties permitted a sampling of only seven rookeries.

A summary of data collected during 1980-86 with the ordinary ratio, jackknife ratio, and regression estimates of the ratio of pups to breeding males appears in Table 2. The estimates based on the three methods are approximately equal within each year; in most cases, the jackknife estimate lies between the ordinary ratio and regression estimates. Estimates of the total number of pups born were obtained by adding counts of dead pups to number of pups alive at the time of census (based on jackknife ratios); approximate 95% confidence intervals were calculated (Table 2).

In Figure 4, estimated 95% confidence intervals

TABLE 2.—Summary of the total number of breeding northern fur seal males, ratios of the number of pups alive at the time of sampling to the number of breeding males counted, estimated number of pups alive at the time of sampling, counted number of dead pups, and estimated number of pups born, and approximate 95% confidence interval based on the jackknife standard errors, St. Paul Island, 1980-84.

Year	Total no. of breeding males	Ratios of pups to breeding males			Number of pups		
		Jackknife ratio	Ordinary ratio	Regression	Live	Dead	Born
1980	5,490	35.695	35.896	35.580	195,966	7,859	203,825 ± 36,838
1981	5,120	33.720	33.821	33.563	172,646	6,798	179,444 ± 20,054
1982	5,767	34.035	33.896	34.147	196,280	7,301	203,581 ± 9,665
1983	4,827	33.135	32.766	33.448	159,944	5,997	165,941 ± 19,216
1984	4,803	34.803	33.861	34.167	167,159	6,115	173,274 ± 22,531
1985	4,372	40.482	40.292	41.071	176,992	5,226	182,258 ± 18,887
1986	4,603	34.735	34.936	34.498	167,656	7,771	167,656 ± 16,272

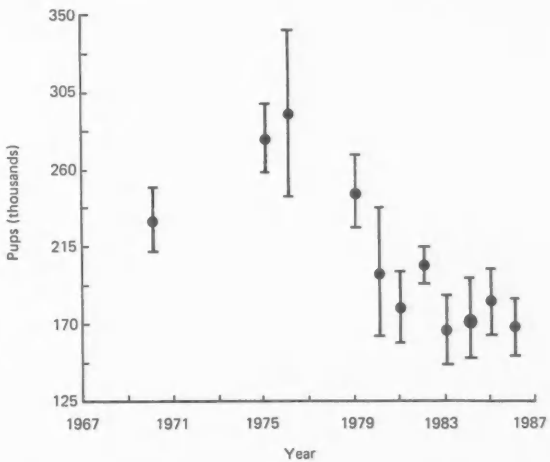

FIGURE 4.—Approximate 95% confidence intervals and estimates of numbers of northern fur seal pups born on St. Paul Island, AK, 1970-86. (We include only those years for which data were available to compute estimates according to the methods developed in this paper.)

of numbers of northern fur seal pups born on St. Paul Island since 1970 are presented; estimates for 1970-79 are based on data from Lander (1980). We computed estimates for those years in which censuses were made on all rookeries or for which data were available to compute estimates according to the methods developed in this paper. Regressions of logarithms of numbers of pups born versus time indicated a statistically significant decrease during 1975-81—a decrease of 7.5% per year with a standard error of 2%. During 1981-86, there is no statistically significant decreasing or increasing trend; the estimate of the slope is −1.8% with a standard error of 1.8%. This slope is statistically different from the −7.5% slope calculated for 1975-81 ($P > 0.90$).

DISCUSSION

Our study indicates that we can obtain reasonable estimates of the total number of northern fur seal pups born from subsampling as few as four rookeries of St. Paul Island if estimates of numbers of pups and breeding males are available for the sample rookeries and if a total bull count is available for the island. Subsampling is successful because within a given year, pup production is predictably proportional to numbers of breeding males. Some refinements in the reduction of bias and variance can be made by restricting the subsamples to stratified designs over large, medium, and small rookeries.

The advantages of subsampling rookeries for censusing northern fur seal numbers are considerable. Most important is the reduction of total disturbance on the northern fur seal population on the island. Our sampling schedule over several years attempts to apportion disturbance approximately equally so that rookeries are neither under- or oversampled through time. This is an important aspect of the sampling design, since it is not known how great the long-term impact of disturbance is. In addition, subsampling requires a smaller crew for the shearing and less time for resampling, resulting in considerable savings of resources.

Ratios of numbers of males to pups, and consequently breeding females, vary considerably over time, even in successive years. It is difficult to interpret the meaning of these changes. During the period covered by Figure 1 (1912-22), numbers of pups born on St. Paul Island were increasing rather rapidly. Since males begin to breed at an older age than females, part of the increase in the ratio of breeding males to pups may be explained by the number of breeding males lagging a few years behind the number of breeding females. Significantly different ratios from one year to the next could also be due to differences in counting methods or abilities among individual counters, or to different survival rates among separate cohorts (e.g., harvest rates). Figures 1 and 2 also imply a certain consistency and a rather uniform rate of usage of rookeries by breeding males and females, in that, if a rookery accounts for 10% of breeding males within a year, it will account for approximately 10% of the total pup production within the same year. A rookery's relative contribution to both these populations may change but the correlation between them does not appear to change.

The recent history of the population of numbers of pups on St. Paul Island in Figure 4 shows a decrease of about 7.5% per year during 1975-81. No significant trend is detectable after 1981, although the number born in 1982 was significantly higher than in 1981 or 1983-86. The causes of the decline are unknown. There is no evidence that pregnancy rates have changed significantly since the 1950's (Goebel and Gentry 1984[4]). Thus, considerable attention has centered on potential causes of increased mortality of northern fur seals: entanglement in debris (e.g., Fowler 1985), effects of weather (Trites 1984; York 1985[5]), and direct effects on food availability from competition with fisheries in the North Pacific Ocean (York and Hartley 1981; Swartzman and Harr 1983; Kajimura 1984; Loughlin and Livingston 1985[6]). One may also speculate that the pattern of decline and possible stabilization in numbers of pups born resulted from a new disease which abated or was controlled by an immune response of the population (c.f., Geraci et al. 1982).

Of the aforementioned explanations for the decline, only entanglement has been cited as a major contributing factor with an attributed mortality of

[4]Goebel, M. E., and R. L. Gentry. 1984. The use of longitudinal records of tagged females to estimate fur seals survival and pregnancy rates. Unpubl. manuscr. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115. (Background paper submitted to the 27th Annual Meeting of the Standing Scientific Committee of the North Pacific Fur Seal Commission, March-April 1984. Moscow, U.S.S.R.)

[5]York, A. E. 1985. Forecast of the 1985 harvest on St. Paul Island. Unpubl. manuscr. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115. (Background paper submitted to the 28th Annual Meeting of the Standing Scientific Subcommittee of the North Pacific Fur Seal Commission, March-April 1985, Tokyo, Japan.)

[6]Loughlin, T. R., and P. A. Livingston (editors). 1986. Summary of joint research on the diets of northern fur seals and fish in the Bering Sea during 1985. NWAFC Processed Report 86-19, 92 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

about 5.5% per year (Fowler 1985). It is possible that entanglement in debris was indeed responsible for the decline during 1975-81, however, the data in Figure 4 do not seem to support this hypothesis. If entanglement were the principal cause of this decline, we would have expected the population to have continued to decrease at the pre-1981 rate since the observed entanglement rates have remained stable since 1976.

We may never know the cause of the 1975-81 decline in northern fur seal production. In general, estimates of population size are highly variable so several censuses are required to detect a statistically significant decrease in a population; thus, the fact of a decline, unless it is sudden and dramatic, is not usually known for several years following its initiation. Post facto studies are invariably subject to criticism for flaws in experimental design; thus, careful continual monitoring of the many aspects of the biology of a population is the best hope for ascribing a particular cause to a population change. Comparisons of the population dynamics, food habits, incidence of diseases, and entanglement rates of northern fur seals with other pinniped species which share their habitat in the North Pacific Ocean might shed additional light on the various hypotheses.

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LITERATURE CITED

CHAPMAN, D. G.
1964. A critical study of the Pribilof fur seal estimates. Fish. Bull., U.S. 63:657-669.
1973. Spawner recruit models and estimation of the level of maximum sustainable catch. Rapp. P.-v. Réun. Cons. int. Explor. Mer 164:325-332.

CHAPMAN, D. G., AND A. M. JOHNSON.
1968. Estimation of fur seal pup populations by randomized sampling. Trans. Am. Fish. Soc. 97:264-270.

COCHRAN, W. G.
1977. Sampling Techniques. 3d ed. John Wiley and Sons, N.Y., 428 p.

DRAPER, N. R., AND H. SMITH.
1966. Applied regression analysis. John Wiley and Sons, N.Y., 407 p.

FOWLER, C. W.
1985. An evaluation of the role of entanglement in the population dynamics of northern fur seals on the Pribilof Islands. *In* R. S. Shomura and H. O. Yoshida (editors), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii, p. 291-307. U.S. Dep. Commer., NOAA Tech. Memo. NMFS SWFC-54.

GERACI, J. P., D. J. ST. AUBEN, I. K. BARKER, R. G. WEBSTER, V. S. HINSHAW, W. J. BEAN, H. L. RUHNKE, J. H. PRESCOTT, G. EARLY, A. S. BAKER, S. MADOFF, AND R. T. SCHOOLEY.
1982. Mass mortality of harbor seals: Pneumonia associated with influenza A virus. Science (Wash., D.C.) 215:1129-1131.

KAJIMURA, H.
1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*; in the Eastern North Pacific Ocean and Eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-779, 49 p.

KENYON, K. W., V. B. SCHEFFER, AND D. G. CHAPMAN.
1954. A population study of the Alaskan fur seal herd. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Wildl. 12, 77 p.

LANDER, R. H. (editor).
1980. Summary of northern fur seal data and collection procedures. Volume I: land data of the United States and Soviet Union (excluding tag and recovery records). U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-31, 315 p.

MOSTELLER, F., AND J. W. TUKEY.
1977. Data analysis and regression. Addison-Wesley Publ. Co., Reading, MA, 588 p.

PARKER, G. H.
1946. The world expands; recollections of a biologist. Harvard Univ. Press, Cambridge, MA, p. 112-116.

SWARTZMAN, G. L., AND R. T. HAAR.
1983. Interactions between fur seal populations and fisheries in the Bering Sea. Fish. Bull., U.S. 81:121-132.

TRITES, A. W.
1984. Population dynamics of the Pribilof Islands North Pacific fur seal (*Callorhinus ursinus*). M.S. Thesis, Univ. British Columbia, Vancouver, 123 p.

YORK, A. E., AND J. R. HARTLEY.
1981. Pup population following harvest of female northern fur seals. Can. J. Fish. Aquat. Sci. 38:84-90.

NOTES

LABORATORY STUDIES OF THE PATTERN OF REPRODUCTION OF THE ISOPOD CRUSTACEAN *IDOTEA BALTICA*

The isopod *Idotea baltica* is a cosmopolitan species that can be an important component of fishes' diets in the field (summarized in Sywula 1964 and Strong and Daborn 1979). Tinturier-Hamelin (1963) reported that *I. baltica* extends along all European coasts, from Finland to Gibraltar, including Great Britain; it is present in the Baltic, the Mediterranean, and the Black and Caspian Seas. In North America it is present from Nova Scotia to North Carolina. In addition, Sywula (1964) reported that it is also found in South America, Bermuda and Barbados, the Red Sea, Australia, New Zealand, and Java.

Investigators who have observed *I. baltica* in the field have reported the species' association with the dominant plants of the community. Interestingly, the type of associated plant varies with geographic locality. In Nova Scotia it is found on *Ascophyllum nodosum* (Strong 1978), in the Baltic on *Fucus vesiculosus* (Salemaa 1979), in Poland on *Zostera* (Mobius 1873, as reported in Sywula 1964), and on *Ulva lactuca* in Jamaica Bay, NY (present study). Generally, the animals' principal food is the plant on which they are found, and this species is often the principal primary consumer of its community (Strong and Daborn 1979), occupying a critical link in local fish food chains.

The present study was undertaken to provide information about *I. baltica*'s reproductive behavior and physiology under laboratory conditions in order to determine the feasibility of developing it as a fish food for mariculture systems.

Materials and Methods

All animals were collected in July and August 1985, by removing attached *Ulva lactuca* thalli from the fouling community attached to submerged piers at the Barrens Island Marina, Jamaica Bay. The animals were sorted from these collections in the laboratory, and placed in individual 22.5 cm diameter glass culture dishes of ambient seawater (29 ppt) either in heterosexual pairs (30 pairs), or in isosexual pairs (20 male and 20 female isosexual pairs). The pairs were maintained at room temperature ($\bar{x}$ = 24.3 ± 2°C SD), with a light cycle of 15:9 L:D. They were fed *Ulva lactuca* thalli ad libitum. These pairs were observed 2 times a day, 12 hours apart, in the light, and maintained until one of the members of the pair died. Observations consisted of noting the occurrence of molts and ovulations, as well as any reproductive behaviors exhibited.

Intermolt periods were calculated by counting the number of days between the first and second molts only of animals maintained in heterosexual pairs. This was done to minimize any artifacts of culture conditions.

In addition to the pairs, 60 females were isolated in individual 10 cm diameter culture dishes. These females were used to determine the variability in timing of molts, ovulations, and expression of reproductive behavior. Females were observed at 12-h intervals, and the dates and times of their molts noted. Males were introduced either on the day the females molted, on day 1 or day 2 after the molts, or no males were introduced at all (12, 19, 13, and 16 different females observed, respectively). The occurrence and timing of copulations, ovulations, and subsequent brood developments were noted for all four groups of females.

Finally, to determine the timing of copulation with respect to the sequence of the shedding of the two parts (see following section) of the female's exoskeleton, males were introduced to five females between the first and second partial molts and the males' responses noted.

Results

Molts

Intermolt periods.—Individuals of both sexes molted repeatedly until they died. Some females molted four times in succession. The average intermolt period of the females was 13.4 ± 0.8 SD days (n = 17, range = 12-15 days); for the males it was 13.0 ± 4.4 days (n = 15, range = 7.5-23.0 days). There was no significant difference between the sexes (Student's t-test; t = 0.24, df = 30, $P > 0.05$).

Nature of the molts.—The exoskeleta of both sexes were cast off the same way. First the posterior half of the exoskeleton (from the fifth segment back) was shed, then the remaining anterior portion was cast off. The anterior part included the first four pairs

of oostegites of the female's brood pouch; the posterior part included the fifth and last pair. There was an interval between the shedding of the two parts (females: $\bar{x}$ = 6.5 ± 6.1 SD hours, n = 35, range = 0-12 hours; males: $\bar{x}$ = 8.3 ± 6.9 SD hours, n = 36, range = 0-24 hours). There was no significant difference between the intervals of the two sexes (Student's t-test: t = 1.41, df = 69, $P < 0.05$). Finally, the observations suggest that there is no terminal molt in either sex, because all individuals molted until they died.

Amplexus

Males picked up and held onto females until the females molted. During amplexus, females were held ventral to the male, and only the males' movements resulted in locomotion. There was no specialized point of attachment on the female. The male inserted the angle formed by the dactyl held slightly extended from the palm of its second gnathopod into the space between the curved, lateral edges of the female's first and second pereonal segments. Sometimes males held onto females with posterior pereiopods as well, but this was only for brief periods of time.

The occurrence of amplexus was correlated principally with female intermolt stage. Amplexus began about $\bar{x}$ = 1.9 ± 1.4 SD days before the female molt (n = 15, range = 0.0-4.5 days) and all couples separated within 12 hours after the female discarded its anterior cast. Thus, females were in amplexus for approximately the latter 14.2% of their intermolt periods.

Most females were in amplexus 24 hours before their posterior molts and separated from the males 24 hours after their anterior molts (Table 1; Fisher's exact probability test, $P < 0.001$). In contrast, most males were not in amplexus either before or after their molts (Table 1; 83.3% and 64.3% not in amplexus before and after the molt, respectively). However, there was a significantly greater proportion of males in amplexus after than before their molts (χ^2_1 = 3.94, $P < 0.05$). Thus, amplexus was principally correlated with female intermolt stage, but male intermolt stage had an affect as well.

Finally, amplexus was never observed in either male or female isosexual pairs.

TABLE 1.—Frequencies of occurrences of amplexus 12 hours before the posterior molt and 12 hours after the anterior molt in *Idotea baltica* maintained in heterosexual pairs.

		Before		After	
Sex	Number of molts	Number in amplexus	Number apart	Number in amplexus	Number apart
Females	33	31	2	1	32
Males	42	7	35	15	27

Copulations

During copulation the male held the female's body in a perpendicular, ventral position, and inserted its pleopods into the posterior part of the female's brood pouch about five times in rapid succession. This was followed by a rest period of about 5 seconds during which the male retained its hold on the female. Then the sequence was repeated two or three more times.

Copulations occurred within minutes after males were introduced to females that had shed both parts of their exoskeleta, regardless of how many days ago the molt had occurred. In contrast, no copulations occurred in the five females that had just molted the posterior portions. Amplexus was initiated with these females instead, and copulation occurred only after the anterior portion of the exoskeleton was shed.

Ovulations

Isolated females ovulated about 2.9 ± 0.5 SD days after their molts (n = 14, range = 2-3.5 days). In contrast, females maintained with males in heterosexual pairs ovulated $\bar{x}$ = 0.12 ± 0.2 SD days after their anterior molts (n = 26, range = 0-0.5 days). The difference was significant (Student's t-test: t = 25.92, df = 38, $P < 0.001$). Another difference between isolated females and females maintained in heterosexual pairs was that none of the broods of the former group developed, while most of the latter broods did (Table 2: 0 of 14 vs. 24 of 26 broods, respectively; Fisher's exact probability test: $P < 0.001$). Eggs ovulated by isolated females were no longer observed in the brood pouches about 5.0 ± 1.8 SD days after the females' molt (n = 12, range = 3-6 days) or about 2.0 ± 1.5 SD days after ovula-

TABLE 2.—Frequencies of ovulations and viable broods of isolated females and females paired with males.

		Number of		Number of ovulated broods that	
	No. of females	ovulations	no ovulations	develop	do not develop
Isolated females	16	14	2	0	14
Paired females	26	26	0	24	2

tion (n = 12, range = 0.5-5.0 days). These observations show 1) that females ovulate in the absence of a male, but 2) delay their ovulations under those conditions; and 3) such eggs disappear from the brood pouches a few days after ovulation.

The introduction of a male to a female any time during the approximately 3-d period that females could delay their ovulations stimulated ovulation. Copulations generally occurred within 5 minutes after males were introduced to females 0, 1, or 2 days past their molts, and all ovulations occurred within 3 hours of copulation. There was no significant difference in the frequencies of copulations and ovulations among females isolated for different lengths of time (Table 3; $\chi^2_2 = 0.008$, $P > 0.05$ and $\chi^2_2 = 0.712$, $P > 0.05$ for copulations and ovulations, respectively).

In contrast, the broods of females who copulated and ovulated 0 and 1 day after their molts developed significantly more often than did the broods of 2-d postmolt females (Table 3; $\chi^2_1 = 3.61$, $P < 0.05$). This suggests that unfertilized eggs aged past 2 days have reduced viability.

TABLE 3.—Frequencies of copulations, ovulations, and viable broods of isolated females introduced to males 0, 1, and 2 days past the females' molts.

Days after molt	No. of females	Number of					
		Copulations		Ovulations		Broods that develop	
		Yes	No	Yes	No	Yes	No
0	12	10	2	10	2	10	2
1	19	16	3	14	5	12	7
2	13	11	2	11	2	5	8

Discussion

The present study has shown that males and females remain apart until towards the end of the female intermolt period, when amplexus is begun. This continues until the female molts, when copulation, followed by ovulation occurs. Females repeated this cycle in the laboratory until they died. Some females produced three broods in succession, without a rest period. In contrast, females in the field in Nova Scotia produce only one brood (Strong 1978), and in the northern Baltic most have one brood (although some may have two (Salemaa 1979)).

It is impossible to say whether the difference in the number of broods produced in the field and in the laboratory is caused by environmental and/or genetic differences. In support of the first explanation, a recent symposium has demonstrated the importance of photoperiod in regulating the timing of reproductive activities of marine animals (Marcus 1986), and, specifically, in the number of broods of some peracarids (Steele and Steele 1986). The photoperiod of Nova Scotia may limit the number of broods there. In support of the second explanation, Healy and O'Neill (1984) noted that two populations of *I. granulosum* produced different numbers of broods in Ireland and in Britain, although there was no significant difference in temperature or latitude at the two locations. Further, while Tinturier-Hamelin (1963) found no reproductive barriers among *I. baltica* from different parts of Europe that were hybridized in the laboratory, she did conclude that the subspecies were genetically distinct. Only laboratory culture, under identical conditions, of representatives from different geographic localities will reveal whether the difference in the number of broods is genetic.

The present observations also reveal that *I. baltica* females spend relatively little of their intermolt periods in heterosexual pairs (14%) compared with other peracarids (the mean of seven other peracarids was 32% (Borowsky 1986)). Strong (1978) reported that a short amplexus period was correlated with a high risk of fish predation in the amphipod *Hyallela azteca* and suggested that couples are more visible than single individuals. This may be the case here as well. Fish and predaceous shrimp are abundant in the community from which individuals for the present study were collected (D. Franz pers. commun.[1]).

Both sexes cast off the posterior parts of their exoskeleta before the anterior parts. Since the female's anterior portion includes most of the brood pouch, the new marsupium is not completely exposed until both parts are shed. Males did not copulate with females that had not molted the anterior cast. The sequence of molts and copulation makes sense, because the present study shows that copulations stimulate ovulations. If copulation occurred before the anterior portion of the pouch were shed, the new eggs might be secreted into the old brood pouch, and then discarded along with the anterior molt.

The present study reveals some flexibility in the timing of key reproductive events. Females could copulate until about 36 hours after they cast off their anterior molts without incurring a significant reduction in fecundity. However, if copulation did not occur by about 3 days after their molts, females

[1]D. Franz, Department of Biology, Brooklyn College, City University of New York, Bedford Avenue and Avenue H, Brooklyn, NY 11210, pers. commun. August 1986.

ovulated spontaneously. These eggs did not develop and disappeared from the brood pouches after a few days. Thus, there appears to be no sperm storage in *I. baltica*, and females must be accompanied by a male at the time of their molts to ensure the development of their broods.

One interesting observation was that males engage in amplexus significantly more often after than before their molts. This may be explained by the observation that neurons become detached from the exoskeleton a few days before the molt (Guse 1983). Thus, if contact and/or water-borne pheromones are secreted by receptive female *I. baltica* as they are in some other peracarid females (Borowsky 1984, 1985, 1986), it is possible that the males cannot sense the stimuli produced by females shortly before their own molts, and therefore are less likely to engage in amplexus at that time.

Conclusion

The results of the present study show that *I. baltica* adults can be maintained in the laboratory, and will reproduce freely with minimal effort and at minimal cost. Females fed exclusively on *Ulva lactuca* produced many broods in succession in non-aerated, uncycled water. While further study is necessary to determine whether juveniles will develop under these conditions, and, if so, what the yield will be, the observations reported here suggest the feasibility of culturing this species for fish mariculture systems.

Literature Cited

BOROWSKY, B.
1984. The effects of receptive females' secretions on some reproductive behaviors in the amphipod crustacean *Microdeutopus gryllotalpa* (Costa). Mar. Biol. 84:183-187.
1985. The responses of the amphipod crustacean *Gammarus palustris* to conspecifics' and congenerics' secretions. J. Chem. Ecol. 11:1545-1552.
1986. Laboratory observations of the pattern of reproduction of *Elasmopus levis* (Crustacea: Amphipoda). Mar. Behav. Physiol. 12:245-256.

GUSE, G. W.
1983. Ultrastructure development and molting of the aesthetascs of *Neomysis integer* and *Idotea baltica* (Crustea: Malacostraca). Zoomorphology 103:121-133.

HEALY, B., AND M. O'NEILL.
1984. The life cycle and population dynamics of *Idotea pelagica* and *Idotea granulosa* (Isopoda: Valvifera) in southeast Ireland. J. Mar. Biol. Assoc. U.K. 64:21-33.

MARCUS, N. H.
1986. Introduction to the symposium: photoperiodism in the marine environment. Am. Zool. 26:387-388.

MOBIUS, K.
1873. Die wirbellosen tiere der ostsee. Jahresber. Comm. Wiss. Unters. Dtsch. Meere 2 Kiel.

SALEMAA, H.
1979. Ecology of *Idotea*-spp. isopoda in the northern Baltic. Ophelia 18:133-150.

STEELE, V. J., AND D. H. STEELE.
1986. The influence of photoperiod on the timing of reproductive cycles in *Gammarus* species (Crustacea, Amphipoda). Am. Zool. 26:459-467.

STRONG, K. W.
1978. Breeding and bionomics of *Idotea baltica* (Pallas) (Crustacea: Isopoda). Proc. N.S. Inst. Sci. 28:217-230.

STRONG, K. W., AND G. R. DABORN.
1979. Growth and energy utilization of the intertidal isopod *Idotea baltica* (Crustacea: Isopoda). J. Exp. Mar. Biol. Ecol. 41:101-124.

SYWULA, T.
1964. A study on the taxonomy, ecology and geographical distribution of species of the genus *Idotea fabricius* (Isopoda, Crustacea) in the Polish Baltic. 1. Taxonomical part. 2. Ecological and zoogeographical part. Bull. Soc. Amis Sci. Lett. Poznan ser D 4:141-200.

TINTURIER-HAMELIN, E.
1963. Polychromatisme et determination genetique du sexe chez l'espece polytypique *Idotea baltica* (Pallas) (Isopode Valvifere). Cah. Biol. Mar. 4:473-591.

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OCCURRENCE OF THE FIRST FRESHWATER MIGRATION OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM*, IN THE CONNECTICUT RIVER, MASSACHUSETTS[1]

Occurrence of a freshwater migration of the gizzard shad, *Dorosoma cepedianum* (Lesuer) (Clupeidae), is documented for the first time in a New England river system. Adult gizzard shad were observed and collected at the Connecticut River fishlift facility in Holyoke and upstream in Massachusetts during 1985 and 1986. It is believed that the Connecticut River migrants are derived from a population recently observed in Long Island Sound and already occurring in the Hudson and Connecticut River estuaries and Nantic Bay.

The gizzard shad is a widely distributed species occurring in marine and tidal freshwaters along the

[1]Contribution No. 104 of the Massachusetts Cooperative Fishery Research Unit, which is supported by the U.S. Fish and Wildlife Service, Massachusetts Division of Fisheries and Wildlife, Massachusetts Division of Marine Fisheries, and the University of Massachusetts.

middle, southern, and gulf coasts of eastern North America (Megrey 1979). Landlocked freshwater populations are known from the Mississippi River drainage (Miller 1956; Megrey 1979) and the Great Lakes (Miller 1956, 1960). On the North American Atlantic coast, the gizzard shad has been reliably reported north to northern New Jersey and New York Harbor (Breder 1938; Miller 1956) (Fig. 1).

Recent evidence indicates that the gizzard shad has ventured into the estuaries of certain major rivers draining into Long Island Sound. Dew (1974) reported that the species was first observed in the lower Hudson River estuary at Indian Point (river km 64.5) between 1969 and 1971 (Fig. 1). Subsequent surveys suggested that the lower Hudson River population is increasing and that reproduction was possibly occurring in the estuary (Dew 1974). However, George (1983) believed that the gizzard shad in the lower Hudson River are derived from fish which migrated through the Erie Canal to the Mohawk River and down the Hudson River. If George's (1983) theory is correct then the lower Hudson River population would have been founded by landlocked freshwater animals, and not by migrating "anadromous" adventives from New York Harbor.

Results and Discussion

In the Connecticut River, adult gizzard shad were first observed near the mouth (river km 2.4, Fig. 1) in 1976 by commercial fishermen using gill nets set for American shad, *Alosa sapidissima*, (Whitworth et al. 1980). In 1984 and 1985, gizzard shad

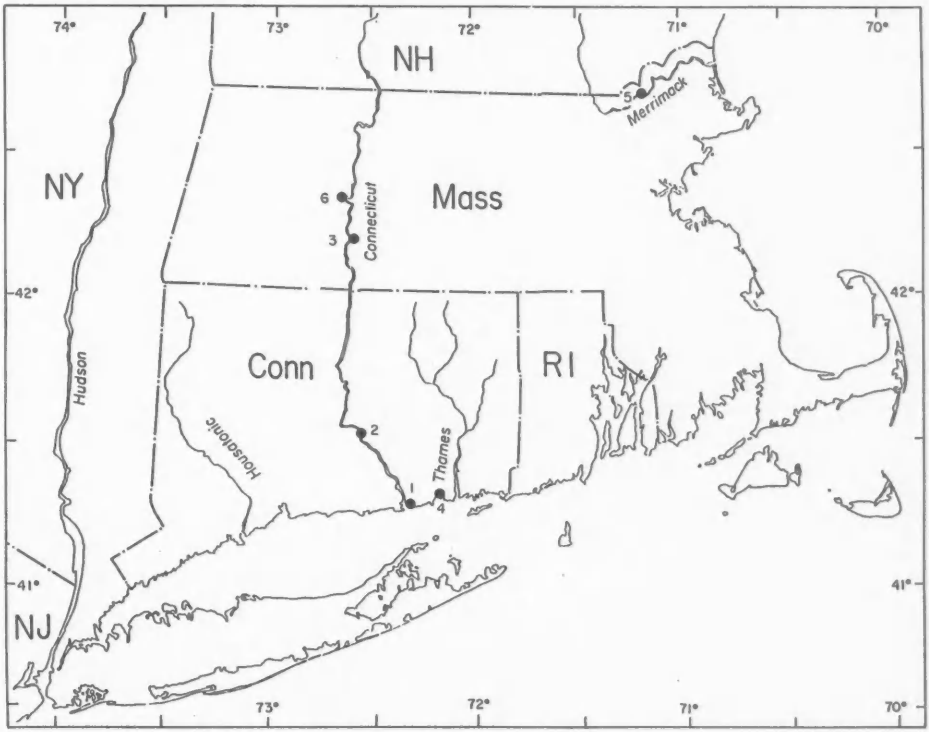

FIGURE 1.—Recent reports of the gizzard shad, *Dorosoma cepedianum*, in New England: 1. Whitworth et al. (1980), Connecticut River, river km 2.4. 2. Gephard (text fn. 2), Connecticut River, river km 26. 3. O'Leary and Smith (this paper), Connecticut River, river km 139.4. 4. Gauthier (text fn. 3), Millstone nuclear power plant. 5. S. Henry (Assistant Aquatic Biologist, Massachusetts Division of Fisheries and Wildlife, Field Headquarters, Route 135, Westboro, MA 01581), Lawrence fishway, Merrimack River. 6. O'Leary and Smith (this paper), Connecticut River, Northampton Oxbow, river km 150.

were subsequently collected by fishermen using gill nets farther up the Connecticut River estuary (river km 26; S. Gephard pers. commun.[2]; Fig. 1) and entrained at the Millstone nuclear power plant in Nantic Bay, CT (C. Gauthier pers. commun.[3]; Fig. 1). In October 1985, a single specimen was captured at the Lawrence fishway on the Merrimack River, Lawrence, MA. This specimen has been deposited into the Museum of Zoology, University of Massachusetts.

During late May and June of 1985 and 1986, over 70 subadult gizzard shad were observed at the Holyoke Dam Fishlift on the Connecticut River in Holyoke, MA (river km 139.4) approximately 69 km above the head of the tide (Fig. 1). Four live and one dead gizzard shad—two females, two males, and one unknown—were collected at the fishlift; all have been deposited into the Museum of Zoology, University of Massachusetts. Mean total length of the live fish was 418 mm (range 395-460 mm) and all were sexually mature. The mean total length of the live fish is near the maximum size reported for this species from freshwater (Miller 1960; Bodola 1965) and larger than the Mohawk River specimens discussed by George (1983). Later in July 1986, a single juvenile gizzard shad (50 mm TL) was captured in the Northampton Oxbow of the Connecticut River (river km 150, T. Savoy pers. commun.[4]; Fig. 1). The specimen is in the collections of the Connecticut Department of Environmental Protection. A follow-up survey in September by O'Leary at the same locality produced no juveniles, but two small adults (300 and 348 mm TL) were captured and these two specimens have been divided among the Museum of Zoology, University of Massachusetts and the Museum of Comparative Zoology, Harvard University. The collected juvenile specimen provides evidence that the species is breeding in the freshwater portion of the Connecticut River, and the co-occurrence of adults suggests that the Northampton Oxbow is an area where reproduction is occurring.

Cooper (1983) suggested that the gizzard shad has been extending its range northward along the east coast of North America in response to warming climate. Whether the species has moved into the Hudson River estuary (Dew 1974) while migrating northward or has entered the river from Lake Erie through the Mohawk River (Erie Canal) (George 1983) is unresolved. The species could have entered the Connecticut River only from the estuary as no inland connection between the Connecticut River and the Great Lakes or the Hudson River exists. The same argument would apply for the origin of other species encountered along the New England coast. The lack of any sightings of gizzard shad prior to 1985 at the Holyoke fishlift leads us to believe that the 1985 and 1986 migrations represent the first indisputable movement into freshwaters of gizzard shad from a marine stock occurring off the southern New England coast. These findings support Cooper's (1983) contention that the gizzard shad is extending its range northward along the eastern North American coastline.

[2]S. Gephard, Fishery Biologist, Marine Fisheries Office, State of Connecticut, Department of Environmental Protection, P.O. Box 248, Waterford, CT 06835, pers. commun. August 1985.

[3]C. Gauthier, Scientist, Northeast Utilities Environmental Laboratory, P.O. Box 128, Waterford, CT 06385, pers. commun. August 1985.

[4]T. Savoy, Fishery Biologist, Marine Fisheries Office, State of Connecticut, Department of Environmental Protection, P.O. Box 248, Waterford, CT 06385, pers. commun. August 1986.

Acknowledgments

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Literature Cited

BODOLA, A.
1965. Life history of the gizzard shad, *Dorosoma cepedianum* (Le Seur), in western Lake Erie. U.S. Fish. Wildl. Serv., Fish Bull. 65:391-425.

BREDER, C. M., JR.
1938. The species of fish in New York Harbor. New York Zool. Soc. Bull. 41:23-29.

COOPER, E. L.
1983. Fishes of Pennsylvania and the Northeastern United States. Pennsylvania State Univ. Press, University Park, 243 p.

DEW, C. B.
1974. Comments on the recent incidence of the gizzard shad *Dorosoma cepedianum* in the lower Hudson River. Third Symposium on Hudson River Ecology, Bear Mountain, NY, Pap. 20, 10 p.

GEORGE, C. J.
1983. Occurrence of the gizzard shad in the lower Mohawk Valley. New York Fish Game J. 30:113-114.

MEGREY, B. A.
1979. *Dorosoma cepedianum* (Lesueur) gizzard shad. *In* D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAlister, and J. R. Stouffer, Jr. (editors), Atlas of North American fishes, p. 69. North Carolina State Museum Natural History, Raleigh.

MILLER, R. R.
1956. Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the

Great Lakes. Trans. Am. Fish. Soc. 86:97-111.

1960. Systematics and biology of the gizzard shad (*Dorosoma cepedianum*) and related fishes. U.S. Fish Wildl. Serv., Fish Bull. 60:371-392.

WHITWORTH, W. R., P. MINTA, AND R. ORCIARI.

1980. Further additions to, and notes on, the freshwater ichthyofauna of Connecticut. *In* P. M. Jacobson (editor), Studies of the ichthyofauna of Connecticut, p. 27-29. Storrs Agricultural Experiment Station, University of Connecticut, Storrs, Bull. 457.

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RELATIONSHIP OF OTOLITH LENGTH TO TOTAL LENGTH IN ROCKFISHES FROM NORTHERN AND CENTRAL CALIFORNIA

Knowing the relationship between otolith length and total length of a fish is useful for two reasons: 1) Fish size can be estimated from otolith lengths measured from otoliths encountered in predator stomachs, in core samples, archaeological sites, etc., and 2) the length of a fish can be verified when the age determined from the otolith lies outside expected values.

The otolith/total length relationship is useful in predator-prey and archeological studies if fish size can be extrapolated from otolith length. Otoliths are often the only part of a prey fish remaining in a predator's gut (Ainley et al. 1981; Treacy and Crawford 1981) or at cooking sites of archeological middens (Fitch 1972). Fish lengths could be estimated from otoliths found as remains of prey or in coastal archaeological excavations (Fitch and Brownell 1968). Existing keys (e.g., Morrow 1979) allow identification of fish species from otoliths. With these keys, personal reference collections, and the length relationships described in this paper, investigators will be able to verify species and size data collected in field sampling, and obtain more complete knowledge of prey species of marine mammals, birds, and fishes.

Large-scale surveys, such as the California cooperative survey (Sen 1984) that samples commercial rockfish landings in northern California, are prone to errors at several levels. Problems that may be encountered in collecting otoliths and measuring fish lengths include errors in recording lengths and the mixing up of otoliths. Some errors can be corrected by measuring the otolith and estimating the size of the fish it came from. Every effort should be made to eliminate erroneous data from the database before curves are constructed or cohort analysis is performed.

In this paper, I report the results of my investigation of the relationship between otolith length and total length for 30 rockfish species of the genus *Sebastes*. Linear regression statistics are presented for all fish of the species encountered.

Methods

Specimens were collected during a life history study on the rockfishes of northern and central California conducted at the Southwest Fisheries Center Tiburon Laboratory. Fish were sampled from the commercial trawl fishery, the commercial sport fishery, skiffs, and research cruises from 1977 to 1980. Specimens were identified to species, and then total lengths of frozen—then thawed—carcasses were measured on a meter board in millimeters (mm). Otoliths were measured to the nearest 0.1 mm with an ocular micrometer. The greatest length of the otolith was measured from the anterior tip to the most posterior projection (Kimura et al. 1979) (Fig. 1) as if the otolith were flat, without compensating for the curvature. Linear regressions were run on total length (y) versus otolith length (x) for 30 rockfish species. Outliers (± 3.0 standard deviations) from the line were assumed to result from measurement or recording errors and were discarded (2% of the observations).

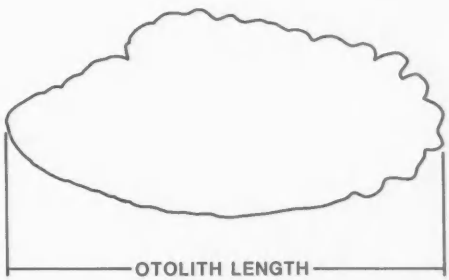

FIGURE 1.—The length of an otolith is measured from the anterior tip to the posterior projection.

Table 1 gives the sample size (N) and the minimum and maximum total lengths used in the analysis for each species and each sex. Table 2 shows estimates of y-intercept (a), slope (b), standard error of estimate ($S_{y.x}$), correlation coefficient (r), and F for each species and sex. Analysis of covariance was used to determine if separate lines for males and females significantly reduced the variance from a common line (Kleinbaum and Kupper 1978). Analysis of covariance was also used to test for significant differences in the relationship of otolith length to total length between the sexes at the $P = 0.05$ level and the $P = 0.01$ level (Table 2). The highest values of r and examination of scattergrams (Fig. 2) indicate that the length relationships are linear over the observed range of values. Limiting the application of these regressions to the ranges of observed values is advised.

TABLE 1.—Sample sizes and size ranges used in the linear regressions of total length versus otolith length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*	Males			Females		
		Total length			Total length	
	N	Minimum	Maximum	*N*	Minimum	Maximum
auriculatus	34	257	477	44	179	523
aurora	27	203	378	44	230	398
carnatus	100	112	289	103	109	279
caurinus	67	281	507	65	135	542
chlorostictus	73	155	450	101	162	458
chrysomelas	72	162	256	94	141	268
constellatus	54	186	422	45	177	430
crameri	42	206	445	47	134	505
diploproa	34	125	343	44	131	381
elongatus	25	188	326	73	135	378
entomelas	38	245	464	68	284	524
flavidus	163	254	504	221	232	539
goodei	26	227	385	52	227	556
hopkinsi	13	119	195	46	134	294
jordani	118	147	281	65	160	321
levis	14	267	773	15	237	900
maliger	13	317	481	21	226	478
melanops	120	334	534	89	197	607
melanostomus	34	250	442	46	297	538
miniatus	64	328	644	35	360	691
mystinus	141	248	480	63	213	375
nebulosus	25	270	391	23	257	500
ovalis	18	228	355	66	241	456
paucispinis	46	287	733	40	296	786
pinniger	92	249	585	81	251	622
rosaceus	72	212	426	75	203	310
ruberrimus	52	257	695	50	245	678
saxicola	29	141	240	73	159	358
semicinctus	15	125	150	16	128	182
serranoides	60	235	469	70	229	528

Results and Discussion

Linear regressions were run on each sex in order to investigate possible sexual differences. In 17 of the 30 species investigated, the relationship between otolith length and fish length is significantly different between males and females (Table 2). Sexual size dimorphism has been observed in 11 of the 17 species in Table 2. These species (plus *S. alutus*) include most commercially and sport-caught rockfishes in the northeastern Pacific Ocean. The six species for which growth curves have yet to be con-

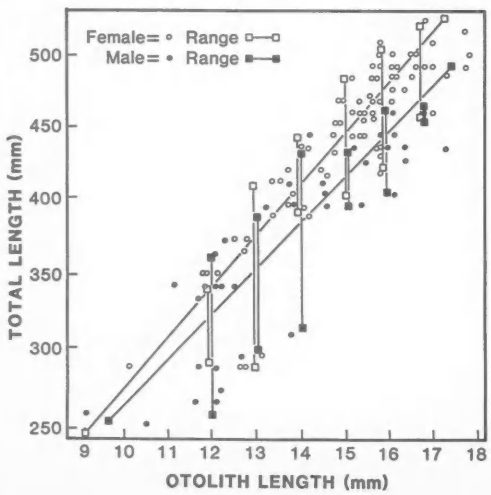

FIGURE 2.—Linear regression of total length on otolith length of widow rockfish, *Sebastes entomelas*. The range of values for males (•-•) and females (o-o) at each whole millimeter of otolith length.

TABLE 2.—Results of linear regressions of total length (y) versus otolith length (x) for *Sebastes*. Measurements are in millimeters. The F-test was run using the sums squared from the analysis of covariance comparing males and females; * - P = 0.05, ** - P = 0.01.

Species of *Sebastes*	Males				Females				
	r	a	b	$S_{y.x}$	r	a	b	$S_{y.x}$	F
crameri[1,2]	0.926	19.270	24.629	22.054	0.988	−43.418	29.440	16.067	4.676*
diploproa[3,2]	0.980	1.282	21.090	12.686	0.985	−22.120	23.717	13.390	6.601**
entomelas[1,2,4]	0.871	−23.039	28.853	33.896	0.880	−51.835	32.452	28.968	6.243**
flavidus[1,2,5,6]	0.923	30.400	23.546	14.771	0.947	−12.604	26.901	18.389	25.637**
goodei[7]	0.975	1.696	23.866	12.741	0.987	−56.831	29.347	16.321	14.842**
hopkinsi	0.868	20.734	20.172	9.567	0.951	−10.895	26.890	10.999	9.172**
maliger	0.840	79.427	21.359	25.533	0.965	−105.649	33.479	19.259	4.221*
melanops[5,6]	0.912	5.472	27.070	18.456	0.949	−124.076	35.784	19.480	25.338**
melanostomus	0.907	−21.094	25.187	21.777	0.918	−21.713	26.211	23.405	8.441**
miniatus	0.961	−42.615	28.385	23.399	0.971	−72.278	30.607	24.103	4.638*
mystinus[6,7]	0.910	−2.255	28.987	23.112	0.881	60.010	22.054	14.965	3.643**
ovalis	0.903	26.185	24.964	13.268	0.963	−27.207	31.859	14.144	21.995**
paucispinis[1,8]	0.893	−51.911	38.441	55.433	0.931	−102.932	43.993	56.501	5.965**
pinniger[1,2,5]	0.950	−61.508	27.663	25.655	0.967	−95.891	30.455	29.004	8.200**
saxicola[1]	0.928	−0.111	19.074	7.544	0.974	−19.565	22.495	12.797	11.412**
semicinctus	0.880	34.331	16.015	4.061	0.938	12.022	21.372	4.981	20.081**
serranoides[6,9]	0.967	−5.307	25.898	13.462	0.969	−63.475	30.445	20.668	10.318**

[1]Westrheim and Harling 1975.
[2]Shaw and Archibald 1981.
[3]Boehlert and Kappenman 1980.
[4]Lenarz 1987.
[5]Six and Horton 1977.
[6]Wyllie Echeverria 1986.
[7]Miller and Geibel 1973.
[8]Wilkins 1980.
[9]Love and Westphal 1981.

structed may also show sexually size-dimorphic growth.

The 13 species with no difference noted between males and females consist primarily of two closely related taxonomic groups (Barsukov 1981). Few growth studies exist for these species. The first group of shallow, nearshore species is represented in this study by *S. auriculatus*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, and *S. nebulosus*. The growth curve for *S. chrysomelas* is the same for males and females (Zaitlan 1986). The second group is the subgenus *Sebastomus* (Chen 1971), represented in this study by *S. chlorostictus*, *S. constellatus*, and *S. rosaceus*. Growth curves exist for two members: *S. helvomaculatus* (Westrheim and Harling 1975) and *S. umbrosus* (Chen 1971), which do not show sexual size dimorphism. The indications are relationships of otolith length to total length reflect the age-at-length relationship between the sexes.

In food-habit studies, otoliths are often found but the sex and length of the fish are not known. Table 3 shows regressions for the combined sexes for those occasions when the sex is unknown or when the regressions were not significantly different between the sexes.

Data analysis for *S. entomelas* shows a potential to derive estimates of age from otolith lengths (Fig. 3). The calculated total lengths for males and females for each 1 mm increment in otolith length are overlaid on the age-length curve (from Lenarz 1987). These relationships are species-specific and

TABLE 3.—Results of linear regressions of total length (y) versus otolith length (x) for *Sebastes* for sexes combined. Measurements are in millimeters.

Species of *Sebastes*	r	a	b	$S_{y.x}$
auriculatus	0.968	−53.032	33.159	17.729
aurora	0.782	15.124	19.910	24.818
carnatus	0.945	−39.365	30.573	10.258
caurinus	0.906	5.099	30.234	26.291
chlorostictus	0.974	−18.537	24.113	14.898
chrysomelas	0.919	−21.780	28.609	9.020
constellatus	0.978	−37.484	25.266	13.123
crameri	0.971	−27.098	28.104	19.912
diploproa	0.980	−12.854	22.635	14.020
elongatus	0.974	−13.564	24.020	12.284
entomelas	0.898	−6.890	33.113	32.247
flavidus	0.938	−10.946	26.506	18.158
goodei	0.983	−57.996	29.129	17.819
hopkinsi	0.957	−30.546	28.868	12.168
jordani	0.985	−2.313	22.096	7.353
levis	0.973	−170.108	47.458	46.975
maliger	0.928	−53.107	29.967	23.862
melanops	0.930	−48.222	30.557	21.002
melanostomus	0.928	−47.070	27.362	23.590
miniatus	0.962	−56.738	29.365	24.516
mystinus	0.912	−18.175	29.765	23.204
nebulosus	0.891	32.970	25.181	16.131
ovalis	0.952	−53.472	33.562	17.179
paucispinis	0.903	−77.089	41.089	59.143
pinniger	0.957	−85.114	29.411	28.398
rosaceus	0.902	−83.484	22.533	10.908
ruberrimus	0.957	−76.233	31.328	31.206
saxicola	0.977	−32.765	23.399	12.663
semicinctus	0.924	−19.182	25.266	6.961
serranoides	0.965	−51.013	29.350	18.965

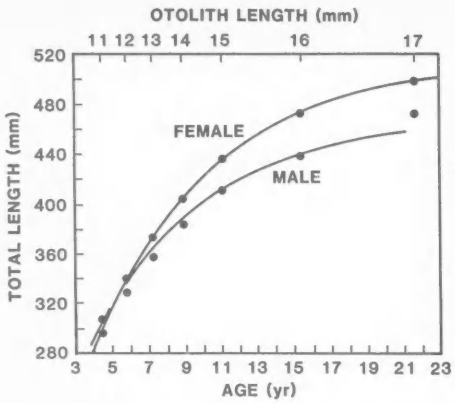

FIGURE 3.—Age-length curve for widow rockfish, *Sebastes entomelas* (from Lenarz 1987). The calculated total length from otolith length is overlaid on the curve to obtain an estimate of age.

should be used within well-defined limits. The scattergram (Fig. 2) with the mean and range of total length found at each 1 mm otolith length increment indicates the ranges within which these data are useful. Some problems in relating otolith length to age include the increased range of fish lengths at older ages and the observed thickening-instead of lengthening of otoliths in *Sebastes* (Boehlert 1985).

These results may be used to estimate total length from an otolith length as shown in the following example. If the otoliths are from fish of unknown sex, the regression statistics from Table 3 would be used to estimate fish length. If the otoliths are from fish of known sex, Table 2 would be consulted. If a species appears in Table 2, the regression statistics for the appropriate sex would be used to estimate fish length. If a species does not appear in Table 2, Table 3 (with regression statistics for males and females combined) would be used. For instance, to estimate fish length from otolith length (OL) for male *S. auriculatus*, the regression statistics from Table 3 are used. An otolith 10.0 mm long gives an estimated total length of

$$TL = a + b\,(OL)$$
$$TL = -53.032 + 33.159(10.0)$$
$$TL = 279 \text{ mm}.$$

Tables have been constructed with the regression statistics presented here. The table for each species (and sex, where appropriate) represents otolith lengths measured in millimeters and the corresponding estimated total length. These tables are available on request from the author.

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Literature Cited

AINLEY, D. G., D. W. ANDERSON, AND P. R. KELLY.
1981. Feeding ecology of marine cormorants in southwestern North America. Condor 83:120-131.

BARSUKOV, V. V.
1981. A brief review of the subfamily Sebastinae. J. Ichthyol. 2(1):1-26. (Engl. Transl. Vopr. Ikhtioi.)

BOEHLERT, G. W.
1985. Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull., U.S. 83:103-117.

BOEHLERT, G. W., AND R. F. KAPPENMAN.
1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. Mar. Ecol. Prog. Ser. 3:1-10.

CHEN, L.-C.
1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. Univ. Calif. 18, 115 p.

FITCH, J. E.
1972. Fish remains, primarily otoliths, from a coastal Indian midden (SLO-2) at Diablo Cove, San Luis Obispo County, California. San Luis Obispo Cty. Archaeol. Soc. Occas. Pap. No. 7:101-120.

FITCH, J. E., AND R. L. BROWNELL, JR.
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. 25:2561-2574.

KIMURA, D. K., R. R. MANDAPAT, AND S. L. OXFORD.
1979. Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*), using otoliths. J. Fish. Res. Board Can. 36:377-383.

KLEINBAUM, D. G., AND L. L. KUPPER.
1978. Applied regression analysis and other multivariable methods. Duxbury Press, North Scituate, MA., 556 p.

LENARZ, W. H.
1987. Aging and growth of widow rockfish. *In* W. H. Lenarz and D. R. Gunderson (editors), Widow rockfish: Proceedings of a Workshop, Tiburon, California, December 11-12, 1980, p. 31-35. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 48.

LOVE, M. S., AND W. V. WESTPHAL.
1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. Fish. Bull., U.S. 79:533-545.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

MORROW, J. E.
1979. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 420, 32 p.
SEN, A. R.
1984. Sampling commercial rockfish landings in California. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-45, 95 p.
SHAW, W., AND C. P. ARCHIBALD.
1981. Length and age data of rockfishes collected from B.C. coastal waters during 1977, 1978, and 1979. Can. Data Rep. Fish. Aquat. Sci. 289, 119 p.
SIX, L. D., AND H. F. HORTON.
1977. Analysis of age determination methods for yellowtail rockfish, canary rockfish, and black rockfish off Oregon. Fish. Bull., U.S. 75:405-414.
TREACY, S. D., AND T. W. CRAWFORD.
1981. Retrieval of otoliths and statoliths from gastrointestinal contents and scats of marine mammals. J. Wildl. Manage. 45:990-993.
WESTRHEIM, S. J., AND W. R. HARLING.
1975. Age-length relationships for 26 scorpaenids in the northeast Pacific Ocean. Can. Fish. Mar. Serv. Tech. Rep. 565, 12 p.
WILKINS, M. E.
1980. Size composition, age composition, and growth of chilipepper, *Sebastes goodei*, and bocaccio, *S. paucispinis*, from the 1977 rockfish survey. Mar. Fish. Rev. 42(3-4):48-53.
WYLLIE ECHEVERRIA, T.
1986. Sexual dimorphism in four species of rockfish genus *Sebastes* (Scorpaenidae). Environ. Biol. Fish. 15:181-190.
ZAITLAN, J. A.
1986. Geographical variation in the life history of *Sebastes chrysomelas*. M.A. Thesis, San Francisco State Univ., San Francisco, CA, 87 p.

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CRATER WOUNDS ON NORTHERN ELEPHANT SEALS: THE COOKIECUTTER SHARK STRIKES AGAIN

A variety of wounds are observed on northern elephant seals, *Mirounga angustirostris*. We report a new type of wound observed on juveniles, primarily from the Mexican islands west of Baja California and rarely from off California. The form and shape of these wounds, and their similarity to wounds reported from other marine mammals, fishes, and squids, suggest that they were caused by a small, squaloid shark of the genus *Isistius*, commonly known as the cookiecutter or cigar shark.

The shape of wounds, their location on the victim's body, the time of the year that the wounds are received, and the age of the seal provide a good indication of the cause. During the breeding season, for example, suckling seal pups bear bite marks on the snout, head, and rump, these having been inflicted by adult females (Le Boeuf and Briggs 1977). Weaned pups and adult females bear fresh bite marks of varying severity caused by adult males biting their necks while attempting to mate with them, and breeding-age males inflict a variety of bite wounds on each other during fights to establish dominance (Le Boeuf and Reiter in press). During winter and spring, *Mirounga angustirostris* of both sexes and all ages exhibit fresh wounds inflicted by white sharks, *Carcharodon carcharias*. The shape and serrated edges of those wounds are easily distinguished from the smooth-edged and halfmoon-shaped wounds caused by boat propellers (Le Boeuf et al. 1982; Tricas and McCosker 1984).

The wounds that we discovered were round, hollowed-out craters, smooth edged at the margin, about the size of a tennis ball, and unlike any of the wounds described above. The similarity in appearance of these wounds to scars inflicted by *Isistius* upon cetaceans (Van Utrecht 1959) and fishes (Jones 1971) implicate the cookiecutter shark as the probable cause. The only reported eastern Pacific occurrence of an *Isistius* is that of an *I. brasiliensis* from off the Galapagos (Compagno 1984). However, we have examined additional eastern Pacific specimens of *I. brasiliensis*, including a specimen from off Isla de Guadalupe.

Background information. Northern elephant seals inhabit traditional island and mainland sites from mid-Baja California, Mexico, to central California. Their range at sea along the Pacific coast is from Isla Cedros, Mexico, to the southern Aleutians. Feeding occurs beyond the continental shelf in deep water (Le Boeuf et al. 1986). It is not known how far from shore they go to feed, but some animals have been seen as far as 3,000 miles away on Midway Island in the mid-Pacific (Condit and Le Boeuf 1984). Several islands are used regularly throughout the year (Guadalupe, San Benito, Cedros, and Coronoados in Mexico and San Miguel, San Nicolas, Año Nuevo, and the Farallones); the sex and age composition of each colony varies with time of year (Le Boeuf and Bonnell 1980). Late August or early September, when most of the observations reported in this paper were made, is the end of the molt period for adult and subadult males and the beginning of the fall haul-out for juveniles, 1-4 years old. Breeding-age males, observed on land at this time, are completing the annual molt, a process that takes

30-40 days; they are in the process of returning to sea to feed. As their number declines, juveniles of both sexes begin to haul-out in increasing numbers. They have been at sea for 4 months or more. Census counts of total northern elephant seals are lower at this time than at any other time of the year (Le Boeuf and Bonnell 1980).

Observations and Methods

Most of the observations were made during an expedition to Mexican islands aboard the MV *Mirage* from 20 to 31 August 1986. Islands surveyed included Isla de Guadalupe, Islas San Benito, Cedros, San Martin, and Los Coronados. We censused northern elephant seals at all sites and, in doing so, recorded the incidence of fresh wounds. On 2 September 1986, we censused and recorded wounds on northern elephant seals at Año Nuevo Island off central California. Similar observations and censuses were conducted weekly at Año Nuevo Island during October and November, when peak numbers of juveniles are observed.

Censuses and inspection for wounds were made from an inflatable 6 m boat, approximately 10 m from seals lying on sandy beaches near the water's edge, or from on foot to get closer to the animals. When possible, we inspected both sides of all seals; we made no attempt to turn animals over to inspect the ventrum or to arouse them to better inspect them for wounds. Approximately half of the animals counted were seen from only one side. Thus, the counts of wounded animals we present are clearly underestimates of the true figure. We noted the location of all wounds and estimated their size and freshness.

We examined preserved specimens of *Isistius* housed in the Marine Vertebrates Division of the Scripps Institution of Oceanography (SIO).

Results

We observed fresh wounds on 20 juvenile northern elephant seals on three of the five island groups inspected in August and September (Table 1); there were no elephant seals on Isla San Martín. Four additional wounded juveniles were observed on Año Nuevo Island later in the year. All wounds were fresh, as indicated by their bloody color, and, with one exception, they were of similar size and shape (Fig. 1). The wounds were round and hollowed-out craters; the margin of each wound was smooth. Each wound was about 5-6 cm wide and 3-5 cm deep. One wound, although like the others in most respects, had a flap of skin and blubber still attached. No fresh crater wounds were observed on adult and subadult males.

Most animals had one wound. Wounds were located on various parts of the body (Fig. 1): the side posterior to the flippers, on the ventrum or the back and to either side or on the midline, on the chest and neck, and just behind the ear. Two animals had two wounds and one had three. One animal had two fresh, identical wounds on the dorsal midline at the level of the foreflippers, separated by approximately 3 cm. Another had two wounds 0.3 m apart on its left side. One animal had three wounds: two on the abdomen and one on the ventral surface of the neck.

The incidence of fresh wounds was highest on northern elephant seals inhabiting Isla de Guadalupe (8.4% of the juveniles censused) followed by Isla Cedros and Islas San Benito (Table 1). No wounded

TABLE 1.—Proportion and percentage of fresh crater wounds on northern elephant seals censused on various Mexican and Californian islands during August and September 1986.

Date	Island	Beach or islet	Adult and subadult males	Juveniles
21-24 Aug.	Guadalupe	Pilot Rock Beach	0/34 = 0	7/95 = 7.37
		Barracks Beach	0/19 = 0	3/35 = 8.57
		Twin Canyons	0/10 = 0	6/61 = 9.84
		Sum: all beaches	0/63 = 0	16/191 = 8.38
25-27 Aug.	San Benito	Este	0/10 = 0	1/57 = [1]1.75
		Centro	0/38 = 0	1/127 = 0.79
		Oeste	0/6 = 0	0/51 = 0
		Sum: all islets	0/54 = 0	2/235 = 0.85
28-29 Aug.	Cedros		0/13 = 0	2/45 = 4.44
31 Aug.	Los Coronados		0/1 = 0	0/14 = 0
2 Sept.	Año Nuevo		0/23 = 0	0/200 = 0

[1]Over 90 juveniles were counted but only 57 were observed close enough to document wounds.

animals were observed on Los Coronados during August or on Año Nuevo Island during August and September. However, four juveniles with fresh wounds, among 700 juveniles present, were observed on Año Nuevo Island during four censuses in November (1, 9, and 30 November). One animal, sighted on 1 November 1986, was marked; a 22-mo-old juvenile born on Año Nuevo Point on 11 February 1984 and tagged 1 month later.

As mentioned above, through examination of the holdings of the Scripps Institution of Oceanography Fish Collection, we uncovered additional Pacific specimens of *Isistius brasiliensis*. The eight specimens from seven lots included six males and two females. The largest, a 470 mm (standard length) female (SIO 69-345) with jaw width of 38 mm, was collected by IKMT (Isaacs-Kidd midwater trawl) between the surface and 2,000 m from north of Easter Island (lat. 25°58.5′S, long. 108°50.7′W). Another eastern Pacific specimen (SIO 78-183) is from off Isla de Guadalupe (29°26.5′N, 119°44′W) and was collected by phytoplankton net. The other eastern Pacific specimen (SIO 52-413) is from west of the Galapagos (00°00″, 100°00″W) and was captured at the surface by dip net.

Discussion

The fresh crater wounds we observed on juvenile northern elephant seals resemble those reported on beaked whales, sperm whales, several species of porpoises, and most of the baleen whales (Mackintosh and Wheeler 1929; Van Utrecht 1959), as well as those from a variety of pelagic fishes (Jones 1971) and a nuclear submarine (Johnson 1978). Jones (1971) and others have demonstrated conclusively that those wounds are the result of bites inflicted by the small squaloid shark, *Isistius brasiliensis*, or possibly by its congener, *I. plutodus*. To date, the only Pacific record of *I. plutodus* is from off Okinawa (Compagno 1984), so we therefore presume that the more wide-ranging and topotypical *I. brasiliensis* is the culprit. *Isistius brasiliensis* is epipelagic to bathypelagic and is known from all tropical oceans, extending northward to off Japan and Baja California and southward to Lord Howe Island. It is typically caught by midwater trawl at depths between 85 and 3,500 m; however, it is occasionally found at the surface at night. The shark is thought to be a diurnal vertical migrator, perhaps traveling a distance as great as 2,000-3,000 m in each direction; in so doing, it apparently encounters feeding *Mirounga*. As noted by Compagno (1984, p. 94), *Isistius* is highly specialized as a facultative ectoparasite in its dentition, suctorial lips, and modified pharynx that allow it to attach to the side of large prey, drive its sawlike lower jaw teeth into the skin and flesh of its victim, cut a conical plug of flesh, and then pull itself free with the plug cradled by its scooplike lower jaw and held by the hooklike upper jaw teeth. The scar patterns of juvenile *Mirounga* support the scenario described above. A comparison of jaw width of *Isistius* of known size with the scar patterns observed on *Mirounga* suggests that the attacking sharks were at least 50-60 cm long.

Northern elephant seals would appear to be easy prey for *Isistius*. They are slow swimmers, compared with large pelagic fishes, and they spend 85% of their time at sea underwater at depths of 400-650 m (LeBoeuf et al. 1985; Le Boeuf et al. 1986). Juvenile seals that use Isla de Guadalupe during the fall are evidently most prone to being parasitized. Juvenile seals hauling out on other islands, especially those to the north, are evidently not exposed to *Isistius* to the same degree. Until recently, no fresh crater type wounds were observed on seals at Año Nuevo despite 16 years of observations by B. J. Le Boeuf. Some wounds observed may have been old, healing crater type wounds, suggesting that the animals bearing them may have been immigrants from the south, the predominant direction of dispersal (Bonnell et al. 1979). Fresh crater wounds have not been observed on the northern elephant seals at the Farallones since their breeding began in 1972 (H. Huber, pers. commun.[1]). Le Boeuf never observed fresh crater wounds on northern elephant seals breeding on San Miguel and San Nicolas Islands during 1968-78, despite annual visits to these islands.

Mexican northern elephant seals of juvenile age fall prey to *Isistius* shortly before they haul-out in late August. Le Boeuf and coworkers never observed crater wounds on seals at these Mexican rookeries during the winter breeding season (13 visits since 1968) or summer molt (4 visits). The juveniles may be exposed to *Isistius* while feeding or while returning to the island. The marked difference in distribution of shark wounds is consistent with the observation that Mexican, southern Californian, and central Californian juveniles feed in different locations, and each "subpopulation" feeds north of its birthplace (Condit and Le Boeuf 1984). Juveniles, trapped in fishing gear, have been caught around 200 m below the surface and captured 16-224 km offshore.

[1]H. Huber, Point Reyes Bird Observatory, 4900 Shoreline Highway, Stinson Beach, CA 94970.

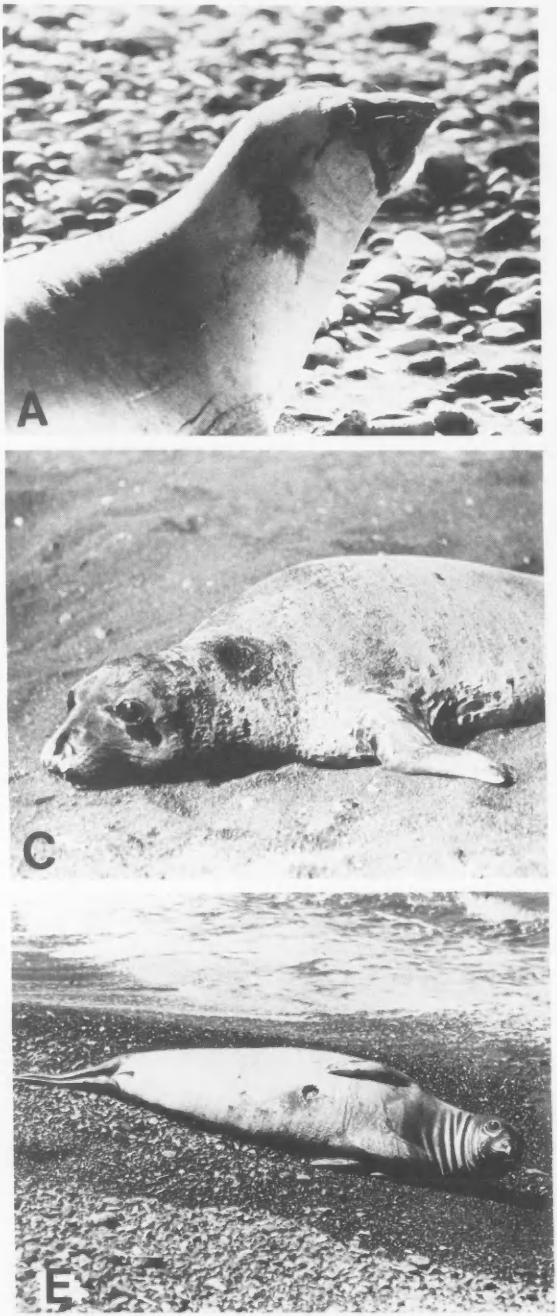
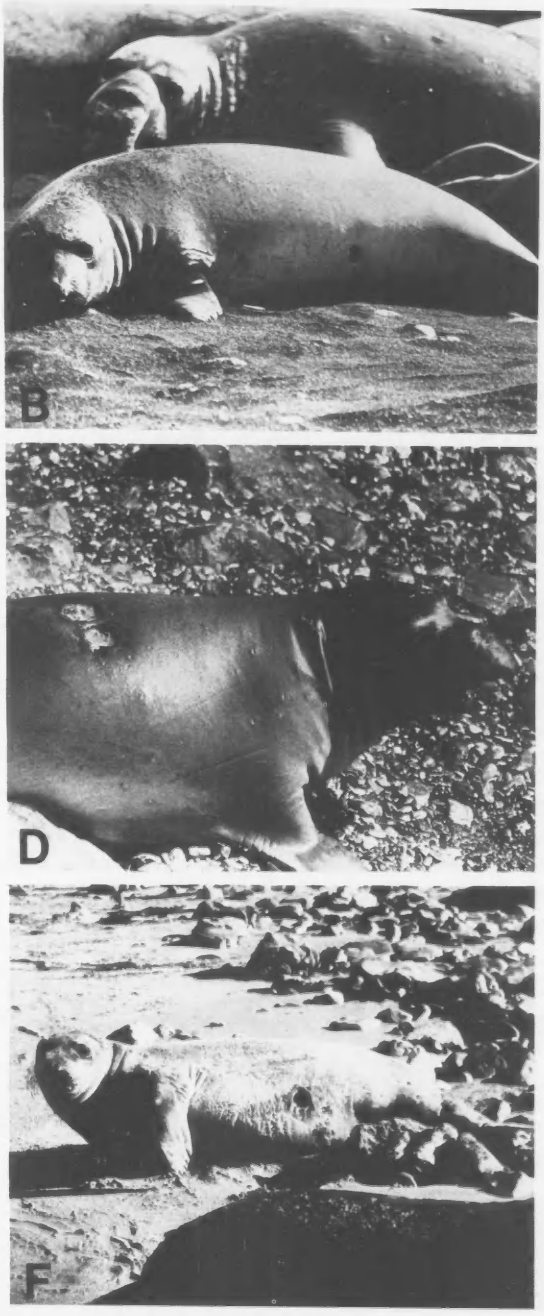


FIGURE 1.—Representative wounds on *Mirounga angustirostris* caused by *Isistius* attacks. A, B, C—taken at Isla de Guadalupe, Mexico; D, E—taken at Isla Este, Islas San Benito, Mexico; F—taken at Año Nuevo Island, California. Not visible in F are two other healing wounds along the animal's right flank. (*Photos A-E by B. J. Le Boeuf; photo F by P. Thorson.*)


B
D
F

That only juvenile northern elephant seals exhibit fresh crater wounds may be explained in several ways. It suggests that this age category is the only one exposed by depth or location to feeding *Isistius*; or, it may suggest that older age classes are able to avoid attack. Another interesting hypothesis concerns the common prey of both *Isistius* and *Mirounga*, midwater squid. It has been speculated that the bioluminescent pattern of *Isistius* might simulate the pattern of a large midwater squid and thereby attract squidophagus predators (Jones 1971) upon which it could prey. It seems unlikely that an *Isistius* could outswim a *Mirounga*; attacks by the shark would thus be accomplished either by attracting the seal, perhaps for a closer inspection of the shark, or by attacking the seal by stealth and surprise. The location of attack scars on the head region of *Mirounga* would indicate a frontal approach, whereas the scars on the back and flanks might indicate that the seal was unaware of the impending attack. Both scenarios are likely. It is also possible that juveniles seals are more readily attracted to the display of *Isistius*, not having learned yet to distinguish them from squid. Further insight into these hypotheses will be provided as more data concerning the spatial and temporal distribution of *Isistius* are collected.

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Literature Cited

Bonnell, M. L., B. J. Le Boeuf, M. O. Peirson, D. H. Dettman, and G. D. Farrens.
1979. Summary report 1975-1978. Marine Mammal and Seabird Surveys of the Southern California Bight Area. Vol. III. Pinnipeds. Bur. Land Manage., Dep. Inter., Contract AA550-CT7-36, 535 p.

Compagno, L. J. V.
1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fish. Synop. 4(1):1-249.

Condit, R. and B. J. Le Boeuf.
1984. Feeding habits and feeding grounds of the northern elephant seal. J. Mammal. 65:281-290.

Johnson, C. S.
1978. Sea creatures and the problem of equipment damage. U.S. Naval Inst. Proc., p. 106-107.

Jones, E. C.
1971. *Isistius brasiliensis*, a squaliod shark, the probable cause of crater wounds on fishes and cetaceans. Fish. Bull., U.S. 69:791-798.

Le Boeuf, B. J., and M. L. Bonnell.
1980. Pinnipeds of the California islands: abundance and distribution. *In* D. M. Power (editor), The California islands: Proceedings of a Multidisciplinary Symposium, p. 475-493. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Le Boeuf, B. J., and K. T. Briggs.
1977. The cost of living in a seal harem. Mammalia 41:167-195.

Le Boeuf, B. J., and J. Reiter.
In press. Lifetime reproductive success in northern elephant seals. *In* T. H. Clutton-Brock (editor), Reproductive Success. Univ. Chicago Press, Chicago.

Le Boeuf, B. J., M. Reidman, and R. S. Keyes.
1982. White shark predation on pinnipeds in California coastal waters. Fish. Bull., U.S. 80:891-895.

Le Boeuf, B. J., D. P. Costa, and A. C. Huntley.
1985. Diving behavior of northern elephant seals. 6th Biennial Conference on Marine Mammals, 22-26 November 1985, Vancouver, British Columbia.

Le Boeuf, B. J., D. P. Costa, A. C. Huntley, G. L. Kooyman, and R. W. Davis.
1986. Pattern and depth of dives in northern elephant seals, *Mirounga angustirostris*. J. Zool. Lond. 208:1-7.

Mackintosh, N. A., and J. F. G. Wheeler.
1929. Southern blue and fin whales. Discovery Rep. 1:257-540.

Tricas, T. C., and J. E. McCosker.
1984. Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. Proc. Calif. Acad. Sci., 43(14):221-238.

Van Utrecht, W. L.
1959. Wounds and scars on the skin of the common porpoise, *Phocaena phocaena* (L.). Mammalia 23:100-122.

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